DEVELOPMENT OF BEHAVIOUR IN THE POUCHED MOUSE
SACCOSTOMUS CAMPESTRIS

by

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FRONTISPIECE

Saccostomus campestris in the grooming posture

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ABSTRACT

Saccostomus campestris is a seasonal breeder and this affects the age at which the female produces her first litter. Increasing the photoperiod and temperature induces fertility in both sexes. Litter size ranged from 2 to 8, with an average of 4,9. The minimum age at sexual maturity was 46 days and the shortest interval between litters 24 days; the gestation period is 21 days. *S. campestris* is born with a dense hair covering but is not precocial. No nipple clinging is present; suckling continued sporadically for 8 weeks, although weaning started at 3 weeks.

There are four natural periods which reflect the critical development of the young. In the neonatal period the tactile response is most strongly developed; huddling is important for protection and warmth. This period is critical for survival as young are totally dependent

on the mother. The transitional period is characterised by a significan increase in motor capabilities, allowing for greater contact between littermates and parents, and thus formation of the first social bonds. During the socialisation period the young become increasingly independent as sight develops; social interactions are increased. The most important factor during the juvenile period is the development of sexual behaviour and aggression.

S. campestris is primarily nocturnal, but is also active during the day. It is an efficient digger and lives in burrows. Hoarding, which is independent of hunger, is strongly developed, and large quantities of hard foods are stored within the nest area; for this purpose it uses the well developed cheek pouches. *S. campestris* explores and forages extensively. Nest building is independent of sex, construction depending on the ambient temperature and number of individuals utilising the nest. Sandbathing, which is also common to both sexes, has both grooming and marking functions.

Breeding was inhibited by female intolerance, which was further aggravated by the restricted space. Conflict was slightly reduced by keeping littermates in pairs. Threat was minimal, and aggression characterised by 'roll ball' fighting. Amicable behaviour between conspecifics was infrequent. The factors indicating the asocial and solitary nature of *S. campestris* are discussed.

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INTRODUCTION

Saccostomus campestris (Peters, 1846) a Murid, of the subfamily Murinae, is indigenous to and widely distributed throughout South Africa, where it occurs in the Southern Savanna Woodlands, South West trial and South West Cape (Davis, 1962; 1974), the Southern African continent (Roberts, 1951; Davis, 1974) and as far north as East Africa (Davis, 1962; Walker, 1964; Hubbard, 1972). Despite its wide distribution, it is not a common species and is infrequently trapped. It appears to have a wide habitat tolerance, occurring in arid as well as well watered regions (Smithers, 1971), although a preference is shown for sandy type soils with sparse vegetation.

In general appearance, Saccostomus is similar to the hamster, with a rotund body, short, strong legs and a short, sparsely haired tail. The ears are rounded and smallish, the eyes large. The ventral surface is white. The dorsal colour varies from a pale grey to brown, as may be expected in a species with such a wide distribution. As in Beamys major (Hanney and Morris, 1962) the hair colour also varies between age groups. Saccostomus is commonly called the pouched mouse or rat, a name it shares with both Beamys major and Cricetomys gambianus, as it is characterised by well formed internal cheek pouches. Although Beamys and Cricetomys having certain morphological similarities, such as size, tail, shape of skull, digits and plantar pads, and also showing a preference for forested regions (Hanney and Morris, 1962), appear to be more closely related to each other than to Saccostomus, these three species have many behavioural characteristics in common, e.g. all three are nocturnal, solitary, burrow dwellers and larder hoarders. They are docile in nature and generally slow moving, which is uncommon among rodents.

Although Saccostomus is primarily nocturnal, in the laboratory activity was frequently observed during daylight. It usually lives in self constructed burrows, but may also utilise other holes (Smithers, 1971). It is a slow moving animal, and as a result frequently falls prey to predators; it also does not appear to be very cautious. Saccostomus eats a wide variety of seeds, including Acacia spp., Combretum spp. and Grewia spp. (Smithers, 1971); termites and other insects have also been found in the pouches (Shortridge, 1934; Roberts, 1951).

The lifespan in the wild is approximately 150 days for the male, and 425 for the female (de Wit, 1972). In the laboratory it may be considerably longer; one individual survived over four years. The sex ratio is 1:1 (de Wit, 1972; Sheppe, 1973).

Saccostomus is commonly used in the laboratory for bilharzia tests (Davis, 1963; Pitchford and Visser, 1970), but little is known about the behaviour and development of this species. That was the primary reason for this study.

MATERIAL AND METHODS

The captive colony, originating from two females which were successfully mated to non-related males, eventually grew to 80 individuals. The original individuals were trapped at Derdepoort, north-western Transvaal between March and April, 1974. From the five individuals trapped at Roodeplaat, near Pretoria, and one obtained from Zululand, no progeny resulted; no wild trapped individuals were successfully mated. During the study 20 females were mated, resulting in a total of 44 litters. Thirty of the matings were between siblings, seven between mother and son and seven between non-related individuals. Most of the breeding stock were kept as monogamous pairs, although some of these pair bonds were of short duration due to the male being killed or badly injured. In such cases a new male was often not tolerated by the female, which prohibited any further breeding from her.

Most of the stock were kept in a room without temperature control and admitting natural daylight. These individuals were housed in rat breeding cages (420 x 250 x 125 mm) with a substrate of sand and woodshavings or ground corncobs. A diet of rat cubes was supplemented regularly with a variety of fruit, vegetables and sunflower seeds. Water and feed were provided _ad lib_.

The parents or female were kept with the young until the female became aggressive towards her litter, or prior to the birth of the subsequent litter, whichever occurred first. Data from 38 litters, comprising 184 young, were analysed. The day of birth was regarded as day 0, and subsequent days were then numbered consecutively.

Further methods are discussed under the relevant chapters.

Chapter 1. POSTNATAL DEVELOPMENT

MATERIAL AND METHODS

Data from 38 litters, comprising 184 young, were analysed. The day of birth was regarded as day 0, and subsequent days were then numbered consecutively. Young were weighed and measured on the day of birth and each subsequent day if possible. Measurements were taken of the head-body length (tip of snout to base of tail), tail length (tail tip to base), ear length (ear notch to furthest tip) and hindfoot length, *cum unguis*. Adult measurements were obtained mostly from dead and euthanased animals, and occasionally from anaesthetised animals. All adults were weighed at least twice monthly over a minimum period of two years.

The techniques used for observing the motor and behavioural development were both experimental and observational.

Testing of the reflexes was performed each day after weighing. Observations were made on animals during reflex testing and in their normal laboratory cages (410 x 245 x 110 mm). Apart from this, observations on behavioural development were performed on animals under a reversed photoperiod, to simulate a more natural environment. Here animals were housed in two aquaria (61 x 32 x 31 cm) and a larger cage (93 x 88 x 59 cm), which were fitted with earth, sand, branches and a nesting box.

Development of the reflexes

Testing of the reflex development was based mostly on the methods employed by Fox (1965), which were later used by Brooks (1972) and Evans (1970), among others.

1. Righting reflex: Young were placed on their backs and manner and speed of righting noted.

2, Rooting reflex: Young were stimulated bilaterally in the facial region, and the strength of rooting recorded. This was measured by the strength with which the young pushed against the fingers or palm.

3. Grasp reflex: The ventral surface of the foot was stimulated with a blunt instrument, usually causing the toes to curl over the instrument. The strength of the grasp (degree of curl) was thus recorded.

4. Negative geotaxis: Young were placed head down on a 45° slope. Ability to turn around and crawl up was recorded. Crawling up showed the presence of negative geotaxis.

5. Cliff drop aversion: Young were placed on a table top, with the forepaws and head over the edge. Aversion was indicated by young turning and crawling away from the edge.

6. Horizontal bar test: Young were placed on a thick, straight branch; ability to walk along it was used to indicate muscular coordination.

7. Postural flexion and extension: Position of limbs was noted when the young were stationary, and held up by the scruff to hang in the air.

8. Contact response: Littermates were placed in a group and after 60 seconds the departure of any young from the group was noted; this was taken to indicate the exploratory urge.

9. Isolation test: Littermates were placed about 10 cm apart and observed for a 5 min period, or until huddling had occurred.

The above responses were graded on a scale of 0 to 10, where 0 represented a non-existent response, with a maximal response of 10.

Vocalisation, posture and all other types of motor activity during the experimental procedures were recorded.

Sensory development

1. Any response, i.e. sniffing, to olfactory stimuli, was recorded.

2. Reaction of animal to touch, or tactile response, was observed.

3. To test development of the thermal response, pups were placed between 2 bottles, each about 50 mm distant. One of the bottles

was filled with warm water (approx. 40°C), and the other with refrigerated water. Direction taken by pup was recorded.

5. Auricular startle response. Response to a short, loud whistle was observed. Initial response to this, or loud banging noises, was taken to indicate the start of auditory function.

Motor and Behavioural development

The start, and final establishment of the following activities into sequences, where applicable, were recorded.

1. Locomotory activity, i.e. crawling, pivoting, walking, running and jumping.
2. Digging and climbing.
3. Sitting on haunches, standing up on hindlegs.
4. Self-grooming, i.e. face washing, scratching and licking.
5. Ingestive behaviour, including pouching and hoarding.
6. Eliminative behaviour.
7. Sandbathing.
8. Any additional motory phenomena, such as tremors and twitches.
9. Exploratory behaviour.

Development of Social Behaviour

Where this type of behaviour comprises any behaviour patterns involving two or more interacting individuals.

1. Contactual behaviour.
2. Agonistic and escape behaviour.
3. Play.
4. Sexual behaviour.
5. Mutual grooming.

RESULTS AND DISCUSSION

MORPHOLOGICAL DEVELOPMENT

Growth

Body mass At birth the young weighed an average of 2,28 g, which represented 2,67 per cent of the mean adult mass of 85,51 g. The minimum average weight per individual of a complete litter at birth was 1,42 g, and the maximum 3,28. There was no apparent tendency for the birthweight of young of small litters to be higher than those of larger litters, as found by Hellwing (1973) and Norris and Adams (1972). The young weighing the most belonged on average to a litter size of four.

Increase in body mass, showing the minimum and maximum mean mass of total litters, is presented in Fig. 1. The loss of mass on day 23 indicates the start of weaning, and subsequent decreases on following days indicate variations during weaning. Suckling did not cease entirely until at least 58 days of age, when one male was observed lying on his back and suckling. Observation of the mammae showed that until young were 22 days old, all mammae were utilized,

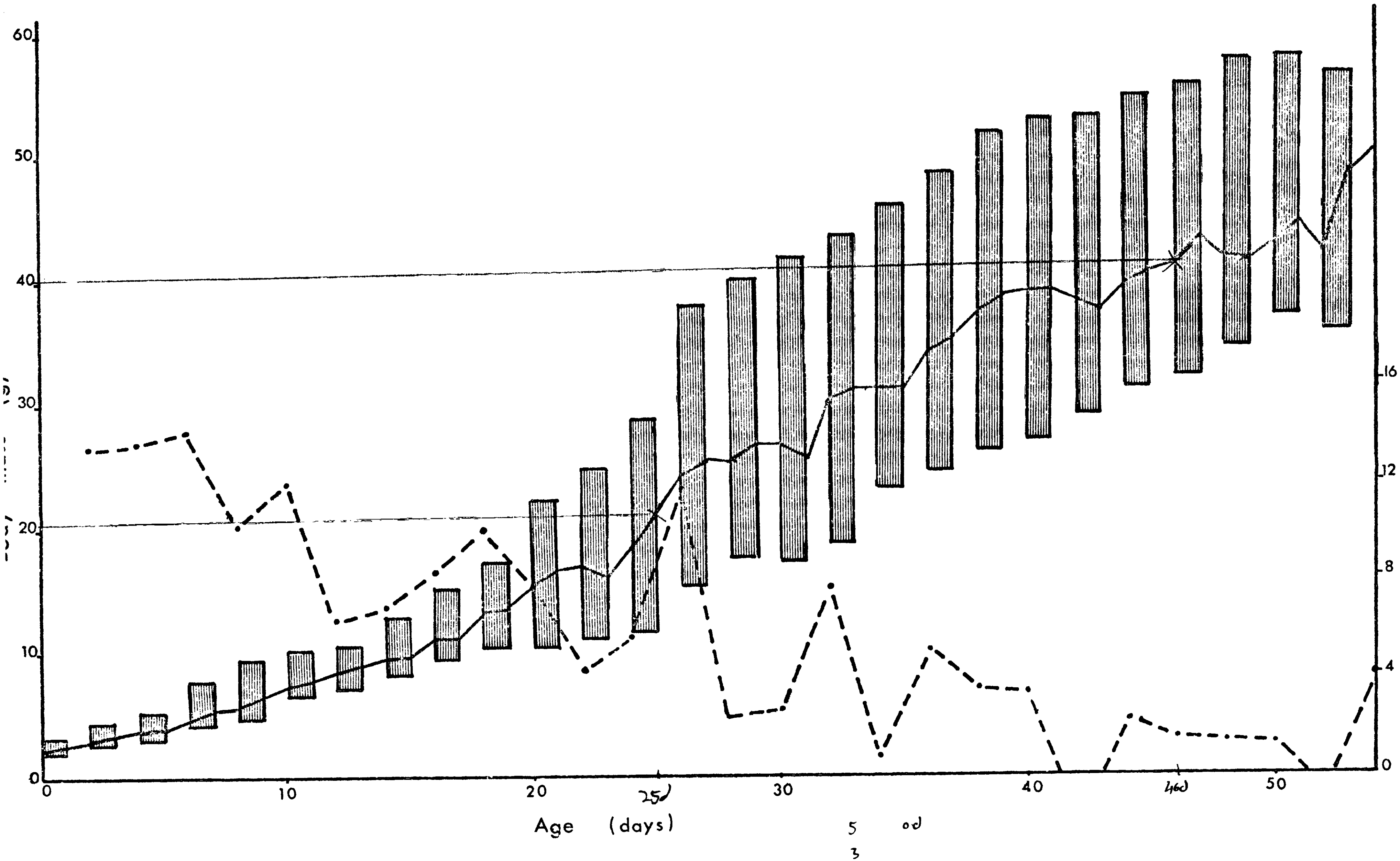

Fig. 1 Mass (full line) and percentage body mass (broken line) increase in S. campestris.

(Shaded area represents range at two-day intervals).

except in some exceptional cases resulting from small litters. This age corresponds closely with the start of weaning. The first mammae to be discarded, at day 23 in some litters, were the two hindmost inguinally situated ones. Suckling was sporadic and ceased at various times as the young grew older, which probably results in the wide fluctuations found in the percentage mass increase (Fig. 1). The greatest percentage mass increase occurred on day 6, which is later than found for most rodents, where the highest mass increase occurred by or on day 4 (Meester 1960, Nel and Stutterheim 1973 and Birkenstock and Nel, 1977). The high increase in mass occurring after day 23 (Fig. 1) was probably due to a greater ingestion of solids following partial weaning.

The young reached 50 per cent of the mean adult mass at 47 days, which is comparable with the growth rate of Desmodillus auricularis, which reached a similar value on day 40 (Nel and Stutterheim, 1973). Aethomys chrysophilus had a slower growth rate (Brooks, 1972) whereas Zelotomys woosnami (Birkenstock and Nel, 1977) and Peromyscus maniculatus (Layne, 1966) had almost reached the adult mass by this time. The growth rate of S. campestris till day 40 is comparable to that found in Mystromys albicaudatus (Meester and Hallett, 1970) apart from the fact that the latter weighed more at birth. The growth rate of S. campestris declined from about 90 days onwards, which is similar to that recorded by Norris and Adams (1971) for Meriones unguiculatus. A few individuals of S. campestris reached the adult mean at 74 days of age. Since sexual maturity had been reached at approximately 60 days of age, the further increase in mass after this time is indicative that

S. campestris continue growing after sexual maturity, as was suggested by Lundholm (1949).

At birth the males were on average slightly heavier (0,38 g) than the females, but a constant divergence in body mass only occurred after 51 days when a male weighed an average 1,19 g more than a female. There were, however, some females that consistently weighed more than males. The sexual divergence in mass increased slightly till adulthood when the males had a mean body mass of 87,68 g and females 83,34 g. There was however, no significant difference ($\alpha = 0,05$, $t = 2,07$) between the body mass of adult males and females. The mass of adults was determined from animals older than 100 days, by which time it tended to stabilise. Adult males (n = 22) had a body mass range of 133,3 g to 48,5 g and females (n = 26) 128,07 g to 49,09 g (Fig. 2). The female monthly mean (this excluded pregnant and lactating females) showed a wider fluctuation than the male mean, with the lowest body mass occurring during the anoestrous phase (Fig. 2). When trapped in the wild, adults weighed considerably less than the mean of laboratory bred animals; those trapped at Roodeplaat near Pretoria weighed 50,75 g ± 7,09 (n = 6) which compares favourably with the approximate mean (50 g) observed by Smithers (1971) for adult *S. campestris* in Botswana. Increased body mass of captive individuals is probably due to the unlimited food supply and restricted activity in a confined space.

Tail The tail at birth measured 13 mm ± 2,51 with a range of 9,6 to 15,2 mm (Fig. 3). The mean value represented 37,24 per cent of the adult mean length of 34,9 mm ± 6,12. Mean tail length found

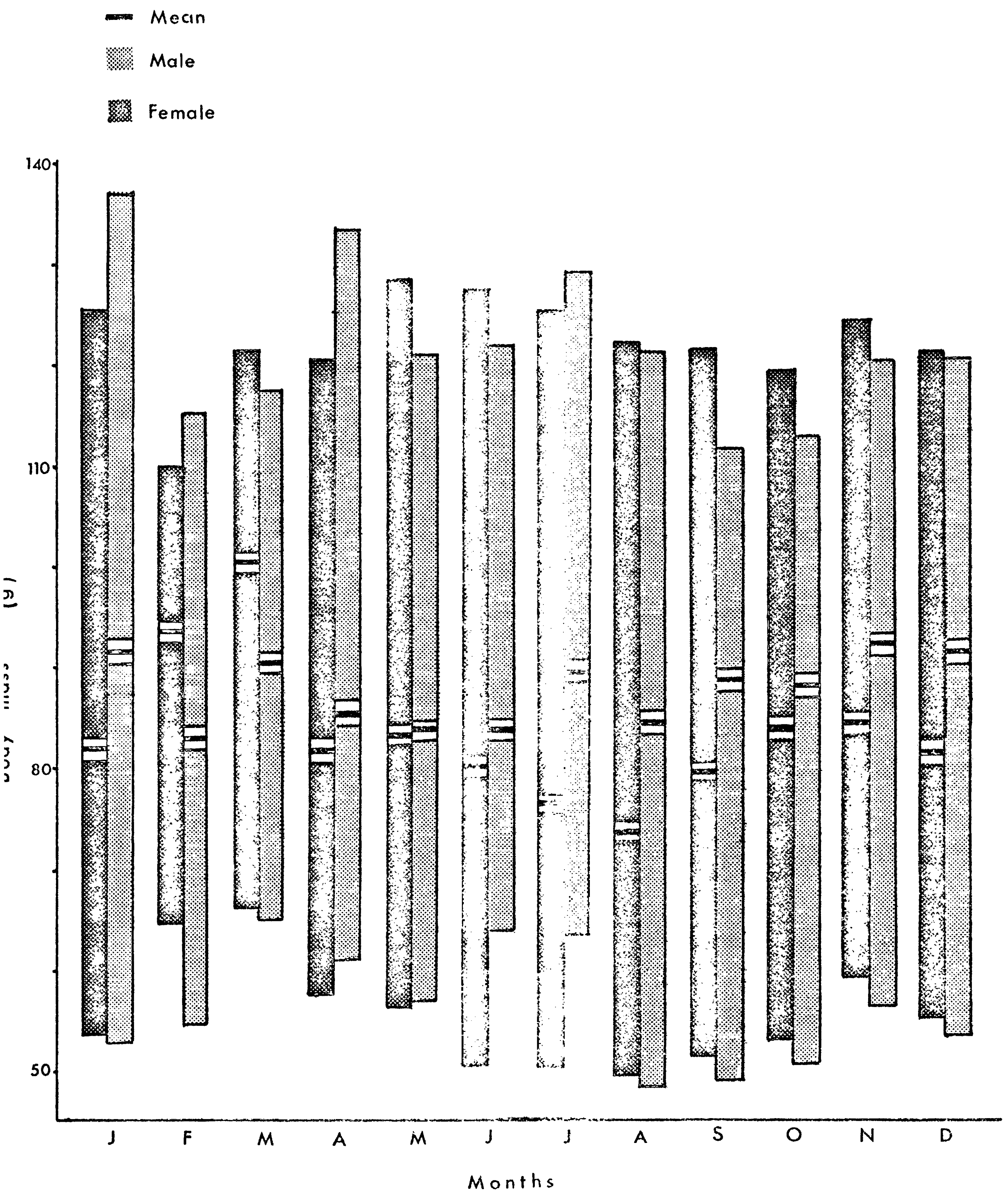

Fig. 2 Mean body mass and range of adult *S.campestris* over a two year period.

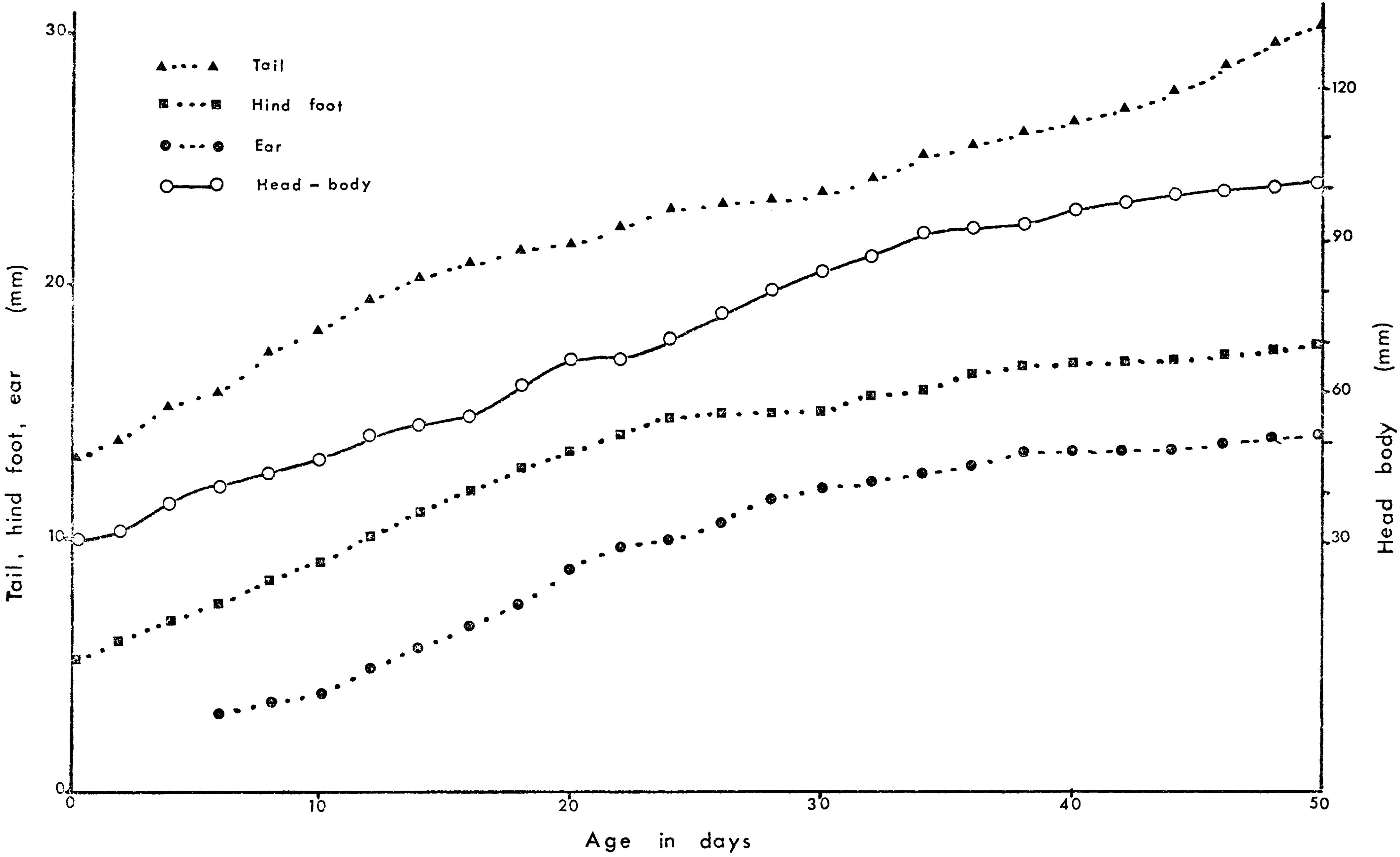

Fig.3 Increase of tail, hind foot, ear and head-body length in S. campestris.

by Lundholm (1950) was 39,88 mm and by Hubbard (1972) 48 mm. Smithers (1971) observed a mean of 44 mm for adult males and 46 mm for adult females. In the present study the females also showed a higher mean (37,3 mm) than the males (34,0 mm). Tail length varied from a minimum of 21,6 mm to a maximum of 45,2 mm.

Hind foot Hind foot length at birth was 4,6 mm ± 0,43, 24,4 per cent of the mean adult value of 18,9 mm ± 0,85. Hubbard (1972) observed an adult value of 19 mm, Lundholm (1950) a mean of 18,6 mm and Smithers (1971) a mean of 20 mm.

Ear Ear length was only measured regularly after the 6th day, when it measured on average 3,1 mm ± 0,46; 17,7 per cent of the adult mean of 17,15 mm. Ears which were erect by the 4th day measured 2,1 mm. Hubbard (1972) recorded a mean adult ear length of 15 mm, Lundholm (1950) a mean of 16,8 mm and Smithers (1971) a mean of 18 mm. It has been suggested that the larger ear size of the Botswana individuals, which inhabit an arid environment, may aid in heat transfer (Smithers, *in litt*).

The growth of the hind feet and ear were at a similar rate (Fig. 3), showing a gradual levelling off at around 36 days of age, whereas the tail growth rate showed a constant increase.

Head and body The average head and body length at birth was 28,9 mm ± 3,0, 25,6 per cent of the adult mean of 113,0 mm. The head and body length varied considerably between adults with a maximum of 147 mm and a minimum of 97 mm. Lundholm (1949) also observed a wide variation, which he attributed to the fact that Saccostomus continues growing after attaining sexual maturity. Hubbard (1972) observed an average head and body length of 112 mm, Lundholm (1950) an average of 118,28 mm and Smithers (1971) an average of 112 mm for males and 109 mm for females. Growth of head and body length is represented in Fig. 3 .

Physical development

S. campestris is a robust animal, with short strong legs, a short, almost hairless tail and it has well developed cheek-pouches. Choate (1972) remarked on its close likeness to hamsters. The dorsal surface is dusky to grey, and the ventral surface white.

Hair proliferation and pigmentation Young were born with a dense covering of hair, with the exception of the feetpads and ear pinnae, although Wrangham (1969) has described them as hairless at birth. This contrasts with most rodents which are born naked apart from vibrissae (Meester and Hallett 1970, Hallett and Meester 1971, Nel and Stutterheim 1973 and Birkenstock and Nel 1977), although Davis (1972) observed that Otomys irroratus were born with head and body well furred, as are also O. angoniensis.

At birth the dorsal hair was dense, light grey and approximately 5 mm in length. This hair extended along the tail, becoming gradually shorter until it was approximately 1,5 mm long at the tail tip. It is probable that no secondary hair growth occurs on the tail, as in adults it is only sparsely haired. The ventral hairs were only slightly shorter and white. The hair on the extremities and tail tip was also white. The hair around the snout was shorter and sparser than elsewhere. Vibrissae (3 mm long) were present, were white and slightly thicker than the normal hair covering but not easily distinguishable.

The dorsal surface skin showed a greyish pigmentation. The ventral surface skin lacked pigmentation and was lightly tinged with pink. It was translucent, so that the internal organs were visible, as also the milk spot. The latter was distinguishable up until the 12th day.

At birth, there was a characteristic light coloured spot on the forehead, with a limited hairgrowth. This spot disappeared within a few hours post partum and it probably represents the fontanelle.

On day 16 the lateral part of the body started to become paler. The dorsal hair in the young was an even, smokey grey colour until approximately 18 days of age, when the tips started becoming buff coloured. At 31 days the young possessed the characteristic adult dorsal hair colour, which is an even smokey grey next to the skin surface, with lighter, buff coloured tips, giving an overall uneven colour appearance. This was similar to the situation found with Beamys major, the pouched rat (Hanney and Morris, 1962). Smithers (1971) also observed that the colour of the haircoat of Saccostomus in Botswana varied between age groups.

The eye area had a characteristic pale marking, the 'goggle' stage which lasted over a week from about day 12 to 21. A paler V-shaped marking appeared just above the snout at about the same time, as did the pale markings behind the ears which are characteristic of adults. The white spot behind the pinnae in Desmodillus auricularis (Nel and Stutterheim 1973) and in Onychomys (Horner and Taylor, 1968) also appear at about this time.

At about 8 days the ear tips became tinged with grey. This tinge is apparently caused by the start of hair proliferation (Hallett and Meester 1971). Hair growth on the ear tips started on day 13, and the ears were fully haired at 19 days. In adults the hair on the ear tips is interspersed with fine white hairs.

Ears At birth the ear pinnae were fleshy and folded down over the external auditory meatus. The pinnae started to detach on the 3rd day, although they remained folded down until the 4th or 5th day, and only became fully erect after the 7th day, although in some individuals this happened a few days earlier. The two pinnae in a given individual did not always loosen simultaneously, and the pinnae of young in the same litter also loosened and became erect at different ages. Unfolding of the ear pinnae does not imply full development of hearing; this fact was also observed by Dieterlen (1963), who stated this to be contrary to eye opening which is strictly correlated with the maturity of a majority of physical characters, and therefore an important gauge of the development phase. The young only reacted to a loud noise (whistle) on day 18, although the meatus was not yet visible. The ear folds started forming on day 16 to 17 and were quite distinct by 23 days of age.

Eyes   At birth the eyes were shut and appeared as a black spot. The eye slit became apparent at approximately 6 days, and by day 10 the eyelid was covered by very fine hairs. In a few individuals the eyes started to open on day 17, but in most not until day 18 to 19, and by day 22 all eyes were open. The eyes started to open from the posterior corner. Both eyes did not always open simultaneously; sometimes this happened a few days apart. It was common to see the young walking around with their eyes shut after the initial opening had occurred. The same was observed on occasion in adults. As *S. campestris* are nocturnal and burrow dwellers, it is possible that their eyes are sensitive to strong light, and this would explain why the young initially walk around with their eyes shut.

Toes   At birth the pads were lightly pink, and the toes were fleshy and fused for half of their length. The toes had well developed straight claws of about 1 mm, which only started to curve on the 4th day. The toes on the forefeet started to loosen a few days before those on the hind feet. Differentiation of toes started on the 3rd day, and those on the forefeet were completely loosened by the 6th to 7th day, while those of the hind feet only loosened on the 9th to 10th day. The tubercles on the forefeet developed sooner than those on the hind feet which started to be more pronounced on day 15.

Incisors   The lower incisors always erupted before the upper, as was the case also with *Z. woosnami*, (Birkenstock and Nel, 1977), *M. albicaudatus* (Hallett and Meester, 1971) and *D. auricularis* (Nel and Stutterheim, 1973). The lower incisors became visible through the gum as early as the 4th to 5th day, and erupted between day 10 to 11. The upper incisors started erupting on the 14th day, when the lower incisors were already on average 1 mm long. By day 22 the molars had erupted and measured approximately 0,05 mm in height.

Appearance The different stages of growth are represented in Figs. 4, 5 and 6. The young animals had a somewhat squat, slightly pear-shaped body, until they started becoming more elongated at about 6 weeks. By three weeks of age the cheek pouch measured 0,6 x 1,4 mm. The adult pouch measures 1,5 x 2,3 mm and extends 15 to 20 mm beyond the external auditory meatus. Small, white bumps, which are thought to be glandular tissue, were only just present in pouches of 3 week old animals. In the adult this tissue covers an area of 0,5 x 1,5 mm, starting just at the inside corner of the lip. Possibly digestive juices, such as in salivary glands, could be secreted to commence digestion in the pouch. The fact that this tissue development coincides approximately with the onset of weaning could be a further indication of the abovementioned function.

MOTOR AND BEHAVIOURAL DEVELOPMENT

Motor and behavioural development is discussed according to the four natural periods as defined by Williams and Scott (1953) for house mice (Fig. 7).

These periods are characterised by major changes, especially in social relationships. These changes are caused by both physiological and morphological changes in the developing young, among others the appearance of sensory functions and the development of motor capacities.

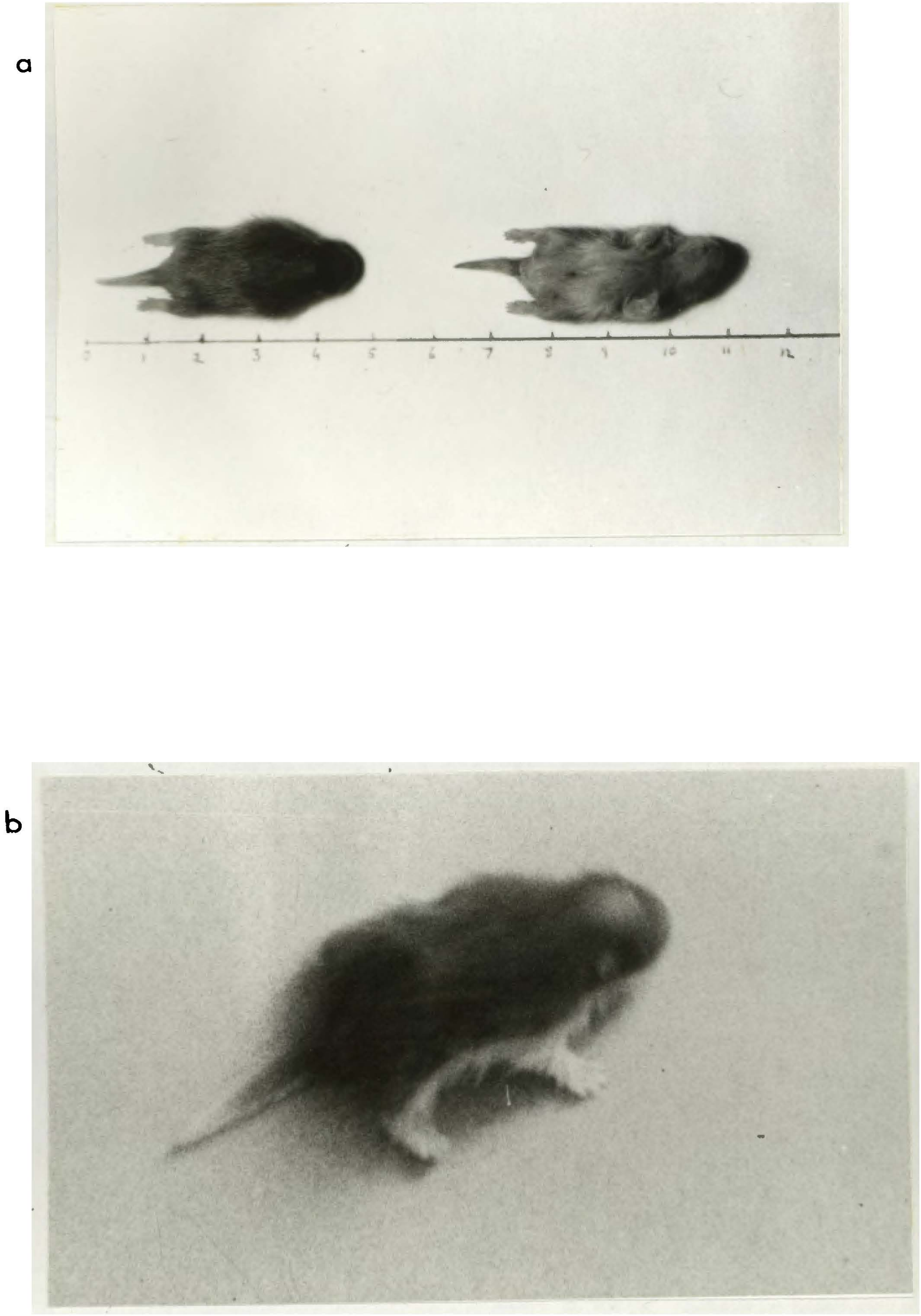

Fig. 4 The development of S. campestris,

a) day 0 and b) day 2.

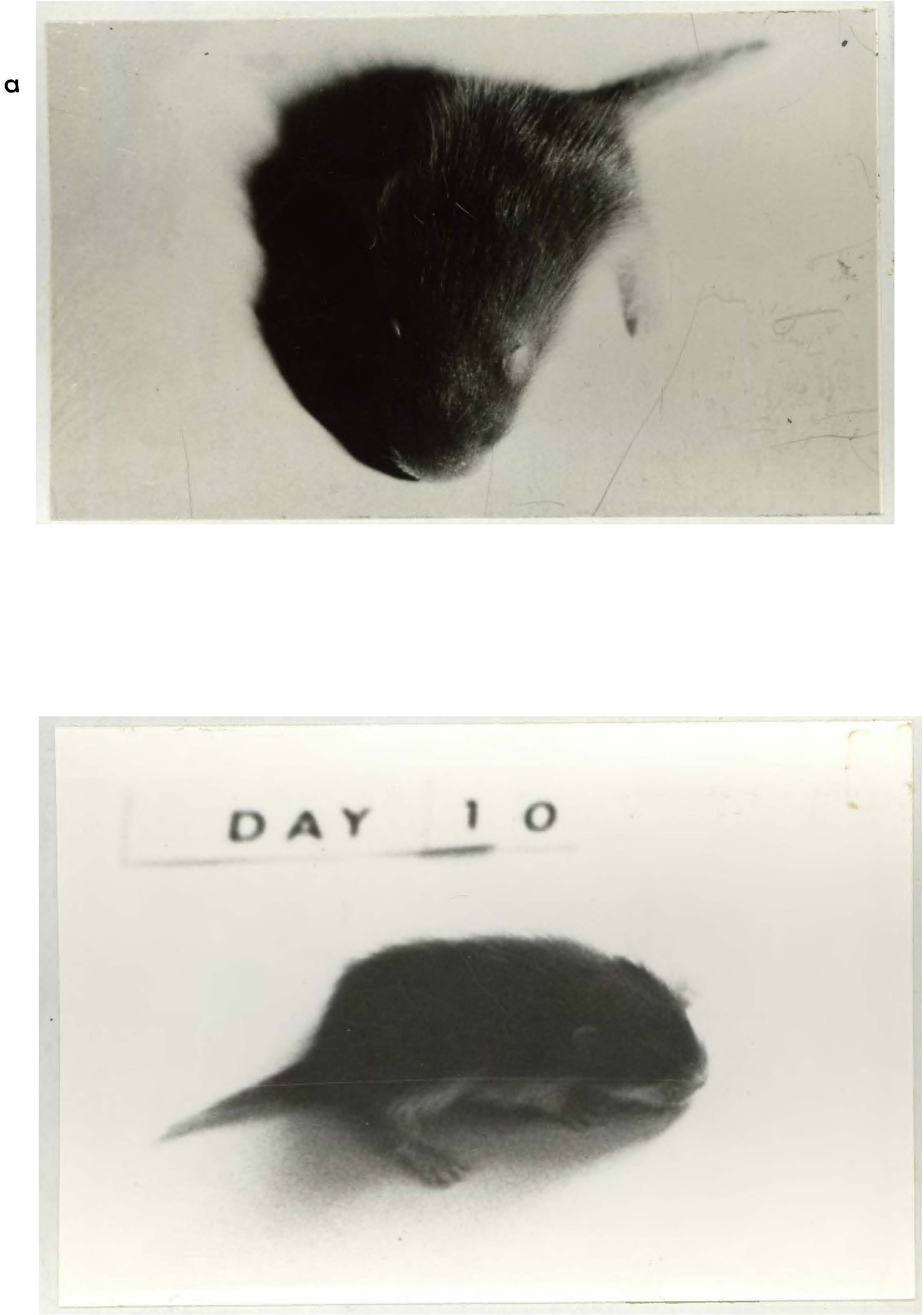

Fig. 5 Further developmental stages of <u>S. campestris</u>

a) day 4 (ear pinnae unfolded) and b) day 10.

Fig. 6 Further development of S. campestris : a) day 15, lick paws; b) day 21, lick paws in grooming posture; c) day 21

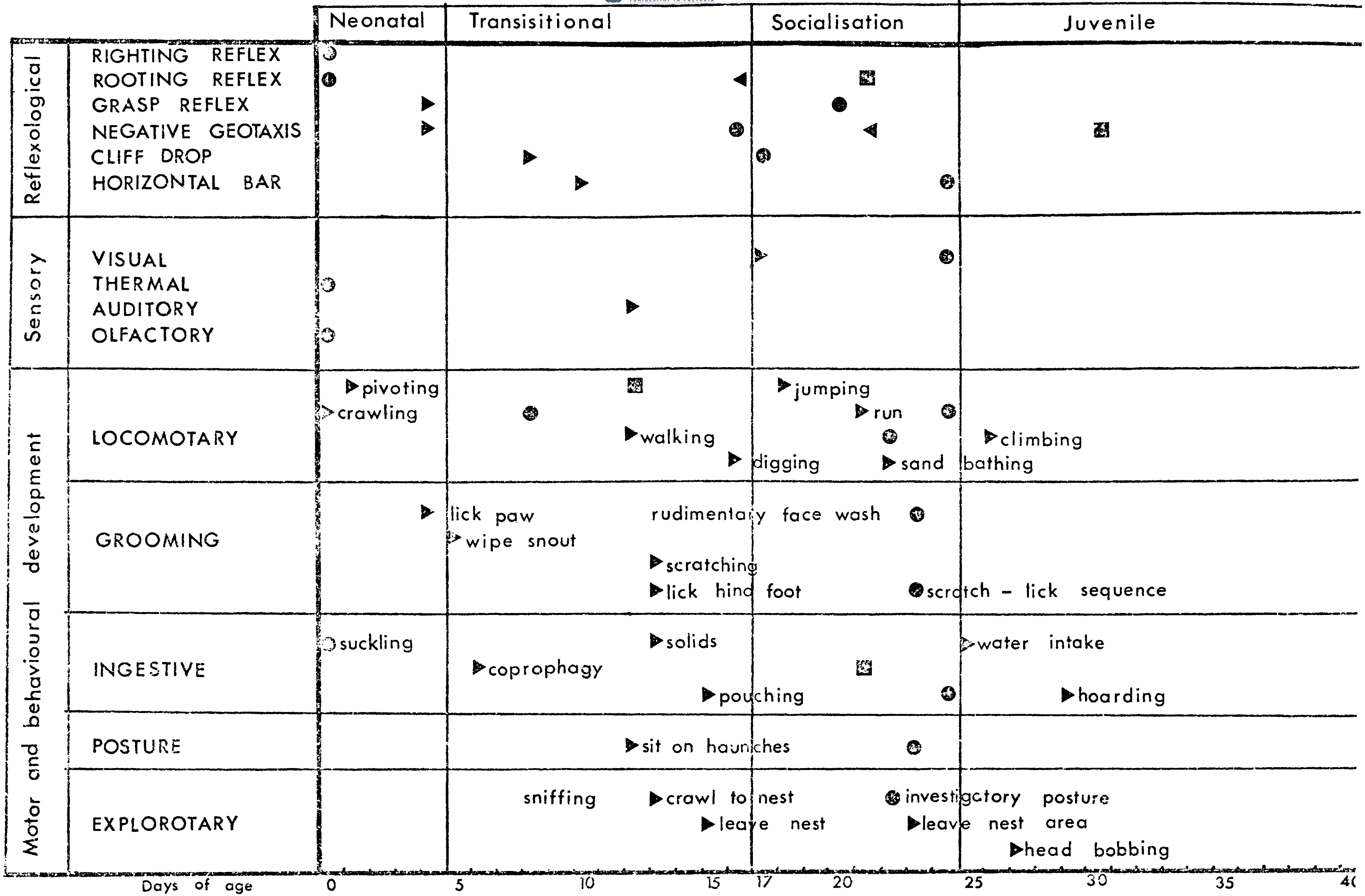

Fig.7 Major developmental aspects of *Saccostomus campestris* till 40 days of age (symbols denote activity start ▶, established ●, decrease ◀ and cessation ▨)

The periods have been adjusted for the different ages of development in Saccostomus campestris, which mature slower than house mice.

The four natural periods are Neonatal (birth to 4 days), Transitional (days 5 to 16), Socialisation period (days 17 to 24) and Juvenile period (day 25 to sexual maturity). Similar phases were used by Baker and Meester (1977) for Praomys natalensis and by Brooks (1972) for Aethomys namaquensis, to describe their respective development.

Period I. Neonatal (Birth to 4 days)

Development occurring mostly in growth and strength, with the appearance of very few overt behaviour patterns which were not present at birth (Williams and Scott, 1953).

Reflexological development

The righting reflex was present at birth. Although the response was strong, the young were very weak, and often unable to right themselves for a considerable time. Frequently, they would turn almost upright, but not have sufficient strength to complete the response, thus rolling back. As the young became physically stronger, so the righting ability became stronger, till by day 5 to 7 the response reached maximal strength. Righting was accomplished by a torsal twist, with the forefeet making contact first. No side preference was apparent.

The rooting reflex, largely a tactile response, was the strongest of all reflexes present at birth, reaching the highest response at about day 4 to 5. Initially, the rooting response was stronger if the young were placed in the palm of the hand, than that evoked by bilateral stimulation of the facial region. In the former the young attempted to 'burrow' into the palm. The possible function could be to bury themselves within the nesting material, or under the litter mates. The same type of 'burrowing' activity was observed by Kirchshoffer (1958) in golden hamsters.

The grasp reflex could only be elicited on the fourth day, but it was very weak and consisted more of an incurving of the toes, than an actual grasp.

Initially, when the young were placed on the 45° slope, they were too weak to crawl up; on the 4th day some young turned around with the intention to crawl up, but were unable to do so. This response indicated the start of negative geotaxis.

During the contact test, young remained in a group, the only response being to huddle closer together. The isolation test was accompanied by squeaking and feeble attempts to crawl, which occasionally resulted in eventual contact and huddling.

Sensory development

The olfactory sense was possibly present at birth, as young lifted their heads and waved them from side to side, possibly sniffing.

Eibl-Eibesfeldt (1951) called this behaviour automatic searching, an instinctive movement, and Eisenberg (1963) defined it as seeking. This zig-zag movement is only performed in the immediate post-natal period, and could be associated with nipple seeking, prior to the full strengthening of the rooting response. Actual sniffing was first noticed on the fourth day.

The strongest response to sensory stimuli was tactile. Initially, from birth till about seven days, young tended to overreact to certain types of contact, as during retrieval and when being held. Overreaction consisted of excessive jerking and wriggling, and was frequently accompanied by distress squeaks. Pups reacted differently, however, and some would remain entirely passive. Strong tactile response was further evidenced by the contactual urge and rooting reflex.

The thermal response was present at birth, although young were frequently too weak to crawl towards the warmth. The response gradually strengthened with age. The young were not able to control body temperature efficiently during the Neonatal period, and quickly became cold if left alone and uncovered.

Development of motor abilities and behaviour patterns

This period was characterised by a general physical weakness and lack of muscular coordination.

Locomotory activity consisted mostly of pushing with the head (rooting), and also a strong pulling action with the forelegs, enabling a feeble crawl. The hind legs remained extended during crawling, and did not appear to contribute to any forward movement. Eibl-Eibesfeldt (1951) suggested that the hind legs are spread laterally to widen the area on which the pups are standing, in order to achieve a better balance. I think it is due to a muscular weakness to draw the legs beneath the body and also a lack of coordination. Furthermore, when the young were suspended by the scruff the forelegs moved in a 'paddling' fashion, while the hind legs remained extended.

During crawling the ventral surface remained touching or close to the substrate. Crawling was in a circular direction, which had the added advantage at this and the next stage of facilitating contact between litter mates, and also of preventing the pups from leaving the nest or nest area.

Pivoting, which involved turning around by using the forelimbs, with the posterior body part acting as a fulcrum, was common. Fox (1965) suggests that pivoting is a primitive type of investigatory behaviour.

The locomotory and manipulative abilities of the forefeet developed prior to those of the hind feet, as is commonly the case in rodents. In fact, Saccostomus campestris have considerably stronger forefeet throughout life, as demonstrated during climbing, and also for the purpose of burrowing.

Self grooming was only observed in a few pups and consisted of the forepaws being held up to the mouth, in a very rudimentary 'lick-paw' motion. This action was seen on the fourth day.

Ingestive behaviour. Only suckling occurred. Young were easily detached from the mother's nipples. Initially, the young lay mostly on their backs during suckling, while the mother remained crouched over them. This serves to protect the young as well as conserving body heat and keeping them warm. As the young got older and bigger, the female started to lie on her side, with legs out in front; young suckled while lying on their stomachs.

Elimination was stimulated by the parental licking of the anal region.

Additional motor activities which occurred were spasmodic twitchings of the whole body, yawning, head quivering and initially 'milk patting' or 'treading' movements, which were not observed in all animals. The latter consisted of alternate pushing movements with the forepaws, as seen in suckling kittens. All the above activities were seen when the animals were lying in the nest, apparently asleep.

Development of Social Behaviour

Eisenberg (1962) defines social behaviour as that comprising any behaviour patterns involving two or more interacting individuals. The predominant form of social interaction occurring during the

Neonatal period was that between mother and young. This is discussed under the separate section on Maternal behaviour.

The second most important form of social interaction occurred during contactual behaviour, which can be defined as activity aimed at maintaining contact among siblings, and with the mother during (and to facilitate) nursing (Williams and Scott, 1953). This behaviour, which involved huddling together, was most marked during the neonatal and transitional periods. The need is the greatest during these two periods as the young are not able to thermoregulate initially. Huddling reduced the total surface exposed, thus minimising heat loss. This behaviour also had the effect of reducing the likelihood of pups straying out of the nest (Ewer, 1968). Huddling was facilitated by the young crawling in circles, as mentioned previously.

Agonistic and Escape behaviour Some young often jerked abruptly and squeaked when they were picked up, or even touched. This could typify a form of escape behaviour. Williams and Scott (1953) observed this type of behaviour in response to pain and disturbance, and suggested an escape behaviour, with an element of aggression. As young grew older they became more passive.

Communication between litter mates was limited to tactile, thermal and probably olfactory stimuli. In communication between litter mates and parents, vocalisation was an added factor. Young were extremely vocal from within a few hours post-partum. The most common sounds during this, and part of the next, period were 'click' and 'chirrup' sounding noises, which were emitted almost continuously when pups were not suckling. The possible effect was to maintain contact with the mother. When the young were picked up or isolated a distress squeal was uttered, though frequently if held in the warmth of the hand, the chirrups were emitted.

The young were fully dependent on the mother during the neonatal period. The most prominent behaviour patterns present in the young are ingestive and contactual. The predominant responses were to control body orientation (thermal response) and to enable nipple seeking (rooting response).

Contrary to the condition in Mus musculus (Williams and Scott, 1953), where the only behaviour pattern not present was sexual, many of the behaviour patterns had not yet appeared.

Williams and Scott (1953) observed that the neonatal period was critical for survival. In Saccostomus deaths occurring during this period were mostly caused by crushing and injury from the parents, as then much fighting occurred. When locomotory ability improved the young were able to move out of the way. The female ate any dead or injured young.

Period 2. Transitional (5 days to 16 days)

This period is characterised by changes in sensory and motor capacities, which enable the development of adult behaviour patterns. It ends immediately prior to eye opening (Williams and Scott, 1953).

Reflexological development

Reactions were still predominantly controlled by tactile and thermal stimuli, although other responses developed due to increased physical strength and muscular coordination.

The righting response reached maximum strength on about the sixth day, and was maintained thereafter.

The rooting response reached maximum strength by the fifth day, and was maintained almost throughout to the end of this period, when it started to decrease. 'Burrowing' in the palm was not so strong as before, but still present.

The strength of the grasp reflex increased on about the sixth day, although it remained moderate throughout the period. The grasping reflex of the forefeet developed prior to that of the hind feet.

Negative geotaxis response became stronger as the young increased in strength and were able to start crawling up the slope. Optimum strength to the response was only reached towards the end of this period.

The cliff drop response was relatively late in developing (about day 8 to 9) and never reached optimum strength. This is possibly due to the fact that Saccostomus burrows, and the ability to avoid heights is not necessary in animals staying on the ground and in burrows, as was suggested by Ewer (1968). In the climbing and agile house mouse the response is already present on the second day (Fox 1965) and in Aethomys chrysophilus (Brooks, 1972) at birth.

Ability to walk along the horizontal bar was present midway through thi period, although young only succeeded in taking a few steps before falling off.

Contact response. Litter mates would still remain in a group initially, but started leaving the group towards the end of the period. This indicated the start of the exploratory urge.

Isolation test. The young still came together and huddled, although as they grew older some would take longer to huddle, due to exploration. On the other hand, other individuals came together quicker, due to improved motor ability.

Sensory development

The only sensory development occurring during this period was hearing. The animals first responded to a loud whistle on the 14th day. The exact onset of hearing ability was, however, difficult to determine, as the young, and all Saccostomus, very seldom reacted to loud noises.

The 'jerky' phase, which is caused by an overreaction to sensory stimuli, became evident. This normally results in the 'scatter' or 'flight' response, as seen in most rodents (Ewer, 1968), and is commonly found in *Praomys natalensis* (Meester, 1960). This type of behaviour occurred infrequently in *Saccostomus*, and then in generally nervous individuals. Normally, *Saccostomus* would merely stand and investigate by sniffing, as was commonly the case with *Mystromys* (Hallett and Meester, 1971). The only feasible explanation is the docility of the animals, making them unafraid.

Development of motor abilities and behaviour patterns

Locomotory development This period was characterised by strengthening of the limbs and increased coordination.

Around day 9 crawling started to become more efficient as the pups started to lift the body off the ground. However, body lift was only maintained after the 13th day. Initially crawling was still inhibited by the splayed hind legs, which were brought totally under the body about the time that walking commenced (day 13). Initially, locomotion was still dominated by circular crawling, which ceased at about day 14. On day 12 improved coordination was shown by the ability of some young to walk along the bar a short distance. Walking was quadrupedal.

Contrary to the situation in mice (Williams and Scott, 1953), the adult locomotory pattern was not achieved during this period, and running did not start till the following period.

Digging with the hind feet was first observed on day 16, showing a further improvement in coordination.

Self grooming The first movement observed in grooming was licking of the paws (day 4 to 5), and face (day 5 to 6). These movements were ineffectual and uncoordinated till towards the end of the period when the face washing sequence was established. At this stage face washing was adequate, although not yet fully adult in manner.

Scratching with the hind leg was first observed on day 13, but the young could not maintain their balance sufficiently at this stage, so that initially scratching frequently occurred whilst the pups were lying on their sides.

Licking of the hind foot was also first seen on day 13. As for scratching, licking was frequently performed with young lying on their sides. Hind foot grooming was the forerunner to the 'scratch-lick' sequence, which was observed in rudimentary form on day 15. Scratching of the body occurred before scratching of the head parts.

In the adult, both of the above grooming sequences are carried out with the animal sitting on its haunches. The latter was first observed on day 12 during face washing, but balance was most precarious and it wasn't till about day 16 that balance could be maintained better, albeit not fully. At this stage the hind legs were spread wide, and the tail rested straight against the ground, both helping to maintain balance.

Licking of the body, apart from that which occurred in allogrooming was not seen, but undoubtedly it would also occur during this period.

Face washing was the most common type of grooming activity to occur during this period, followed by the scratch-lick sequence. Face washing was also the first grooming pattern to emerge, as in Cricetomys (Ewer, 1967). This was in contrast to the situation in Praomys, Otomys and Desmodillus (Baker and Meester, 1977; Davis, 1972; and Nel and Stutterheim, 1973) where scratching occurred first.

Grooming (predominantly 'lick-paw' and face washing) as a displacement activity is common in Saccostomus. It was first observed in the young on day 12, when one pup licked paws during weighing. Thereafter, it occurred fairly often, with a face wash being first observed on day 16.

Ingestive behaviour Nutrition for the first part of the period is obtained by suckling. The practice of larder hoarding permits young to start eating solids sooner (Ewer, 1968); otherwise eating of solids only starts when young leave the nest. Eating of solids (a pellet) was first seen on day 13, approximately two days after incisor eruption, and pouching occurred on day 15. It is possible that the eating of solid food could have occurred earlier, for the young were not always visible in the nest. Initially the young ate in a 'lying-down' posture, resting on their forefeet, with the food resting between the forepaws. Feeding started prior to eye opening. This is the result of having food permanently in the nest, so that the young do not have to forage, which can only be accomplished successfully after eye opening.

Coprophagy was first seen when one young was six days old. It was not observed frequently, but could have occurred more often. In the majority of cases coprophagy was direct, i.e. picked up by a young individual from the mother's anum. On two occasions young were discovered with droppings in the pouch. Coprophagy is commonly observed in many rodents (Dieterlen, 1963; Ewer, 1967) and could be a means of establishing, or helping to establish, the gut flora.

On two occasions young were observed licking or nibbling at the mother's mouth. It is not known whether they were nibbling at some food in her mouth (not visible) or licking her saliva. Saliva licking was found in Cricetomys, and Ewer (1967) suggested that the saliva could possibly contain an enzyme, but the function was not clear.

Eliminative behaviour No sign of droppings in the nest was apparent, so it is probable that all waste matter was still being eaten by the female. In altricial species anogenital stimulation is important to enable young to eliminate; this probably continues till the young leave the nest (Ewer, 1968).

Hyperkinesias (ticks and tremors) were still observed occasionally during this period, but they also frequently occur in adult animals, only when asleep, and are often accompanied by squeaks (possibly they are dreaming). Fox (1965) observed that these tremors coincided with the development of new locomotor abilities, but this would have no bearing on adult animals.

Exploratory behaviour was minimal during this stage. The young made a few tentative attempts to leave the nest on day 15, usually to follow the mother. They never managed to venture far, even if they wanted to, for they were instantly retrieved. Young (during the retrieval test) on a few occasions attempted to follow the female home on day 13. Vigorous sniffing of the environment was first seen on day 9.

Vocalisation, as typical in young animals started to decrease from about the 10th day. There appears to be a correlation between frequency of vocalisation and increasing independance. However, as young apparently do not hear till around the 14th day, the functional significance of this was not apparent between siblings. A similar decrease in vocalisation was also observed in *Peromyscus californicus* (Eisenberg, 1962) but no explanation was offered.

Development of Social Behaviour

Social behaviour during this period was influenced by the increased motor abilities of the young, and their ability to hear.

Contactual behaviour was initially still very strong, and in fact occurred quicker due to improved locomotor ability. The young especially liked to have their ventral surface in contact with a litter mate, causing huddling on top of one another. When the young huddled in this manner, and one pup left the group, or a new one joined, a complete reshuffle would ensue, with individuals 'burrowing' under and climbing over each other, till all were comfortable.

Agonistic and escape behaviour No aggressive behaviour was observed, either towards litter mates, or the handler.

Towards the end of the period a few over-anxious young showed the 'jerky' type of behaviour, as commonly occurred when overreacting to sensory stimuli. This was infrequent, possibly due to the fact that all animals were frequently handled and docile. This period of hypersensitivity and overreaction corresponds closely to the time when the young increase exploratory activity and leave the nest, and therefore could serve as an extra protection prior to sensitization with the environment.

No play or sexual activity was observed.

Mutual grooming, either of young towards parents, and among litter mates, was not common in *Saccostomus*. However, allogrooming was first seen on the 8th day. The most frequent site of mutual grooming was the ear region and the scruff, as was also the case in *Praomys* (Baker and Meester, 1977).

The transitional period was mostly dominated by the physical strengthening of the young, with resultant rapid development of a majority of responses.

The most significant development was the improvement in locomotor ability, which enabled exploratory patterns to emerge, and a corresponding decrease in the contactual urge. This resulted in a significant change in the social behaviour. A transition, although incomplete, to adult methods of nutrition also occurred.

During this period, two of the three factors were present for the critical periods phenomena, as defined by Scott (1962), which occur during development. These represented the optimal period for learning, which coincides with the critical period of primary socialization (i.e. young animals that were handled frequently were less nervous than those not handled). The other factor represented the optimal period for infantile stimulation.

Period 3. Socialization (Age 17 to 24 days)

This period begins with the opening of the eyes and is therefore characterised by the first (visual) social interactions between litter mates, and by an increase in exploratory behaviour (Williams and Scott, 1953).

Reflexological development

A decrease in the rooting response occurred, till finally on the 22nd day it was non-existent. This probably coincided with the physiological weaning age of the young, although young have been observed suckling until day 58.

The grasp reflex was fully developed during this period. The forefeet had a stronger reflex throughout.

Negative geotaxis elicited both minimal and maximal responses. The former was due to the young just climbing/jumping off the slope; on the other hand some animals climbed all the way up.

The cliff drop response reached its maximal value, a score of 7. This was due to the fact that some animals consistently fell off, and during this stage, even jumped off, although it was about one metre to the floor. This indicated further that Saccostomus had little height perception, at this stage any rate.

Ability to walk along the horizontal bar improved although several individuals still fell off. This was not attributed to lack of muscula coordination, but rather poor climbing ability.

There was an increased tendency for pups to leave the group during the contact test. Some young, however, still remained huddling.

When the pups were placed apart for the isolation test, they would spend some time exploring. There was an increase in exploratory activity as the young matured.

Sensory development

With the opening of the eyes, all sensory faculties were established. Olfactory stimuli became more important with the increase in exploratory activity, and also in investigation of litter mates and parents.

The jerky movements, as observed during the previous period, were still occasionally seen. Shillito (1963) suggested that these jerky movements indicated (in the vole) a state of conflict between the exploratory urge and the accompanying reluctance to move into an unfamiliar area. If so, this could further explain why this behaviour was limited in Saccostomus, as they were unafraid and explored boldly.

Development of motor abilities and behaviour patterns

Locomotory development Walking became more efficient and well coordinated. The adult manner of walking was established around day 22.

Young were first observed running at three weeks. This pattern of locomotion developed rapidly, and young ran in an efficient manner by the end of this period. Running occurred most frequently during this and the juvenile period, as it was commonly employed in play activity. Adult Saccostomus are relatively slow runners, especially when compared to the speed of the majority of rodents. Adult Saccostomus showed a preference for walking and were very seldom observed running.

The upright investigatory posture (standing up on the hind legs) appeared at about three weeks, and was seen quite frequently during exploratory activity at the end of this period.

The ability to jump appeared on about day 18.

Digging progressed into the adult sequence of scratching with the forefeet, and kicking the removed earth/sand away with the hind feet. It was considered that digging was also a precursor to sandbathing, as Saccostomus usually dig in the sand prior to sandbathing. The latter was first observed on day 22, although in a more rudimentary form as the roll was not as complete as in adults. The adult pattern of sandbathing matured quickly.

Self grooming All the grooming patterns matured during this stage, apart from the 'scratch-lick' sequence. The adult grooming posture was maintained after the pups were able to maintain their balance in the crouching posture, which is also used during feeding.

'Scratch-lick' sequence was adult in nature, apart from the holding of the hind foot (which had been scratching) with the forepaws in order to lick it clean. This was not observed till day 29, but there is no reason why it should not have occurred sooner.

Extensive scratching of the ear occurred during the beginning of this period. Ewer (1968) suggested that young may experience an itching in the ear during meatus opening. The meatus of Saccostomus was first observed open on day 18, although opening probably occurred sooner.

Ingestive behaviour Young started to hold their food between the forepaws, initially with the forefeet still touching the floor, and later (day 22) in the adult manner, in the crouching posture.

The frequency of nursing diminished at around 22 days, by which time utilization of solids had become more efficient. The decrease in milk intake was noticed because the pups ceased suckling all the nipples; also the duration and frequency of suckling decreased.

Coprophagy was observed for the last time on day 21. Probably the pups no longer required any of the possible nutrients found in adult droppings. On day 20, a dropping was found in the pouch of one young.

Young have been observed to fight over a choice bit of food, and once they had got hold of it to pouch it quickly, presumably to prevent the other pup from obtaining it. Ewer (1966) observed a strong degree of food envy in *Cricetomys* pups, which would always pouch the food quickly for the same reason. This type of behaviour, however, was not so common in *Saccostomus*.

Adults have a manner of pushing at the pouch with the forepaws, either to dislodge food in it, or to settle it more comfortably. This pushing action was seen on day 20 in pups.

Exploratory behaviour Young started adopting the investigatory posture at the beginning of this period. This coincided with the motor development of crouching on the hind limbs, and eventually standing up, which quickly matured (day 20). By day 22 the young could maintain their balance adequately, in the traditional 'investigatory sniff posture'.

By this time (day 23) the young were also ready to leave the nest area and increase the exploratory surface covered. Initially they frequently followed the female home during retrieval; later they started following her out.

Leaving the nest area and cessation of retrieval (day 24) coincided closely (overlapping by a day) as prior to this the young were frequently retrieved as soon as any exploratory activity outside the nest started.

The young were quite bold and unafraid, unlike *Mystromys albicaudatus* (Hallett and Meester, 1971) which would start back to the female at any disturbance.

Development of Social Behaviour

Social contacts prior to this period consisted mostly of huddling between litter mates, and nursing contact with the mother. Now there was an increase in play and mutual grooming behaviour.

The *contactual urge* was much reduced as the tendency to explore increased. The young still huddled during sleeping and resting periods. Huddling was no longer necessary to maintain body heat, but still served to keep the young in a group together.

Agonistic and escape behaviour Aggressive behaviour between litter mates was not yet present during this period, apart from one situation where two pups were fighting quite seriously over a piece of apple (day 21). Choate (1972) observed a 'rolling ball' manner of fighting in juveniles three weeks old. Such behaviour, however, was only observed in mock fighting during play.

Threat posture was only occasionally encountered and occurred for the first time when a pup was startled by a sudden noise.

During this period a very few young tried to escape during handling, one bit me (day 18), but this was the only young ever to attempt to bite.

Play activity was first observed at 19 days of age, and thereafter increased in frequency, only slowly until day 22, when it started to occur more often.

The occurrence of play corresponded closely with the ability to run and jump, and also with eye opening, all essential factors for this activity.

Playing was the predominant form of social interaction which occurred during this period.

Play will be more fully discussed under Juvenile behaviour.

Mutual grooming activity increased slightly during this period.

During this period the young became increasingly independent of parental care, as both suckling and the frequency of parental grooming decreased, and exploratory activity increased.

The behaviour patterns matured quicker during this period than in the previous two periods. Adult coordination in the majority of behavioural sequences was attained, due to maturation of motor capacities.

The most significant occurrence during this period was the opening of the eyes, which caused subsequent noteworthy changes in social interactions. Dieterlen (1963) regarded eye opening as the most critical factor in determining the degree of development, and suggested that it is strictly correlated with the maturity of the majority of physical characteristics, and the start of independence from parents in altricial young, as was the case in *Saccostomus*.

Scott (1962) suggested that contact and emotional arousal result in social attachment. Isolated individuals were always more aggressive. It has not been proved, but isolation at this stage in the young would probably result in increased aggression, as it does at later stages. It is probable that mutual grooming, playing and other contactual behaviour, enable, and strengthen, the formation of a social bond.

The overall activity during this period increased. Kaplan and Hyland (1972) found a high increase in activity of *Meriones unguiculatus* around the time of eye opening which they attributed to an increased arousal of the reticular activating system. In *Saccostomus*, however, the increase in activity was not so drastic, probably due to the fact that they are nocturnal.

Period 4. Juvenile (day 25 to sexual maturity)

All behaviour is essentially adult in nature, except sexual behaviour and care of the young.

Reflexological development

Negative geotaxis   Response to being placed head down on the 45° slope ceased, as the young always jumped off.

All the other responses were established by this stage.

Sensory development

All sensory capacities were well developed. Hearing was acute, as shown by young moving ear pinnae in response to noises. Response to the thermal test ceased as young wandered off to explore.

Development of motor abilities and behaviour patterns

Locomotory development   The only locomotory ability which had not developed prior to this period was climbing, which was first observed o day 26. Climbing activity increased as the need to explore rose. As the young grew older, they would climb on the wire tops of their cages, hanging suspended upside down and moving around in this fashion. This activity was more frequently observed in adults.

Grooming sequences were fully developed by this period. Holding of the hindfoot with the forepaws to groom it after the 'scratch-lick' sequence, was first noticed at 29 days of age, but probably could have occurred earlier.

Ingestive behaviour   Young were observed drinking water from day 25, probably to compensate for decreased liquid intake due to a decrease in the suckling frequency. Nursing was observed till 58 days of age, though some young stopped sooner. Clearly during this period the young were no longer dependent on the mother for nourishment. Nursing was confirmed by both visual sight of pup, and the state of the nipples. The only other rodent to nurse so long is <u>Aethomys</u> (Brooks, 1972) where attachment to the nipples, although infrequent, was observed up to 40 days of age.

Weaning appeared to be voluntary (on the part of the young) and the only obvious explanation for prolonged nursing was that the young obtained a feeling of comfort from it.

Hoarding behaviour was first seen on day 29, although pouching ability had developed long before this. In <u>Cricetomys</u> (Ewer, 1967) hoarding was observed when the young were a month old.

<u>Eliminative behaviour</u> Anogenital stimulation by the mother was no longer necessary to induce elimination. Young were able to deposit waste in the common dropping site, situated outside the nesting area.

<u>Exploratory behaviour</u> reached a peak during this period, and other than play and sleep, was the activity indulged in most often. A juvenile was first observed head bobbing on day 27. Head bobbing consists of a rythmical vertical swaying of the head, and normally occurred when the individual concerned was at a vantage point. It occurred in both sexes, but not very frequently. It is thought this action enables the animal to focus on a distant point, but the exact function is not clear. Stutterheim and Skinner (1973) observed a

sideways swaying of the head, weaving, in _Gerbillurus paeba paeba_ which was apparently a stereotyped reaction, and an escape response.

Development of Social Behaviour

All facets of adult social behaviour, with the maturation of sexual behaviour, were present by the end of this period.

Contactual behaviour   Juveniles would perform most motor activities independently, but when the time came for sleeping and nesting, they liked to huddle. The contactual urge remained throughout their lives, provided they were not separated. It was also stronger in males.

Contactual behaviour, especially in older juveniles and adults, was influenced by the ambient temperature. If it was very hot, the animals would frequently lie stretched out and with a minimum of contact.

Agonistic and escape behaviour   Escape behaviour was limited. Aggressive fighting was first observed at three weeks; it was normally of short duration, and not so intensive as in adults. Aggression between litter mates was generally limited to scuffles. The majority of juvenile fighting appears to be mock fighting as encountered during play activity. During mock fighting, other individuals would frequently join in, which never occurred during earnest fighting.

At approximately seven weeks of age aggression between litter mates increased. This age corresponds closely with the attainment of sexual maturity. However, fighting between siblings was rare. This is attributed to the formation and establishment of a social bond, as is further discussed in social behaviour and aggression.

On a few occasions, during vicious fighting, Saccostomus excreted a very strong-smelling substance with the urine. The same substance was frequently smelt during fighting in hamsters. This substance was first noted in 25 day old young.

Mutual grooming Young still indulged in mutual grooming, although towards the end of the juvenile period the frequency decreased. Mutual grooming in adults was infrequent. Young were occasionally seen to lick their parents.

A behaviour, which is common in Praomys (Meester, 1960), was the 'caring' by a previous litter for the following one. The older young were seen to lick those in the younger litter, but only when these were very young. The older young also attempted to retrieve the younger individuals, but were not very successful as they were still not strong enough to carry them. This behaviour was observed when the older juveniles were about six weeks old.

Play Play does not consist of actions specific only to play, but rather a series of movements derived from other activities (Ewer, 1968; Eibl-Eibesfeldt, 1970). Play is further characterised by the absence of a specific fixed order of actions.

Ewer (1968) noted that play requires a childhood (developmental) period under adult protection, during which the young are not required to look after themselves. As a result in rapidly maturing species there is no time for play. Saccostomus have only a short time under parental care, and although play does occur, it is not very intensive and play bouts are of short duration. Play was never observed in adults or between adults and juveniles.

The most frequent activities eliciting play in young Saccostomus were allogrooming and naso-nasal contacts. Allogrooming usually led to mock fighting, contrary to the situation in Meriones persicus, where the sequence was totally reversed (Eibl-Eibesfeldt, 1951). Nosing either led to a short sequence of allogrooming, followed by play, or directly to play. Play was not elicited by running, as is common in many species, but by initial contact with a conspecific. Wilson (1973) noted that a scent present on the back of the head in voles stimulated play. Therefore, as in Saccostomus, contact was the stimulating factor.

Play in Saccostomus involves some of the fixed action patterns which are part of the sequences occurring during aggressive interactions in adults, but in play they occur independently of their usual function For example, play involves running, chasing and tumbling; in the latter instance one juvenile is usually lying on his back and kicking at the other on top. Mock fighting is distinguished from adult aggression by the absence of biting, threat, and tooth chattering; also more than two individuals may, and usually are, involved. Therefore, patterns which appear during play are not subject to the usual motivating mechanisms.

The fact that aggressive movements are most frequently involved in play may be significant, if, as is commonly believed, learning occurs during play. As aggression is the primary social interaction between strangers of Saccostomus, practise and learning (experience) of this behaviour by juveniles would aid them in later life. However, to obtain proof, the aggressive behaviour of juveniles reared socially and in isolation would have to be compared.

To regard play as practise for adult functions is permissible in Saccostomus, as no play is observed in adults, which presumably need no further practise to perform actions which are now part of their daily behavioural repertoire.

Chapter 2 MATERNAL BEHAVIOUR

The *Saccostomus* female provides food and warmth for her young, grooms and protects them, and introduces them to their first solid food.

SUCKLING AND FEEDING

Development of suckling has been divided into three subsections by Rosenblatt and Lehrman (1963) according to the nature of the behavioural interaction by which suckling is initiated.

'Neonatal phase'. Suckling is mutually initiated. The mother lies over the young continuously during the first 10 to 12 days post-partum, to keep them warm, as they have no thermoregulatory ability. In turn, the rooting reflex of the young is stimulated and they search for the female's nipples. The 'milk tread' releases the milk.

'Mother-young phase'. Suckling frequency is mostly controlled by the female, and suckling is usually initiated by the female. To stop the young suckling, the female may leave the nest, or change position. This phase lasts to the physiological weaning age, at between three to four weeks.

'Young phase'. Suckling is always initiated by the young although it may be stopped by the mother. Suckling during this phase occurs with less frequency. Suckling till the age of 58 days was observed, but it ceased at various ages in different litters.

Suckling in Saccostomus occurs only in the nest. Initially the female crouches over the young, providing warmth and protection as well as nourishment; as the young become older and larger, she lies on her side.

Apart from the usual larder hoard which consists of hard foods, the female starts bringing soft foods to the nest at around 10 to 14 days after giving birth, thus introducing the young to solids. The same behaviour was observed in Cricetomys females (Ewer, 1967). In addition the young of Saccostomus also start nibbling at the food in the larder. Young have also frequently been observed nibbling at food in the mother's mouth, which may be partially digested. (See Pouching).

RETRIEVAL

MATERIAL AND METHODS

Thirteen litters, consisting of a total of 73 young, were used in experiments on retrieval. The young were placed at a point away from the nest, usually 300 mm, and the following were recorded:

(i) Latency period - time from deposition of young till the first retrieval or attempt at retrieval.

(ii) Retrieval time per young - duration of handling by parent.

(iii) Time spent in nest by female between retrievals.

(iv) Time between leaving the nest and initial contact with the young.

(v) Route from retrieval site to nest.

(vi) Grip, number of times each pup was picked up, and the manner in which it was carried.

(vii) Activity other than retrieval indulged in by female during the retrieval period.

(viii) Total retrieval time of litter.

RESULTS AND DISCUSSION

Young were normally retrieved by the female; however, in one case the male repeatedly retrieved the pups, as the female totally ignored them. In this case the male always took the young to the female, even once pushing it under her chin, when the young started wandering away. It was later discovered the female had no front teeth, so possibly she was unable to retrieve. A preparturient female was als observed to retrieve an alien litter, and care for it as if it were her own. After parturition, and especially within the first 2 weeks, lactating females retrieved alien young with no discrimination, apart from the occasional sniff. In a few instances young of an older litter were observed attempting to retrieve young of a following litter, but were unable to lift and carry them. Rowell (1961) observed that retrieval in hamsters was dependent only on sufficient physical strength to pick up the pup.

Young are carried in the mouth, which is the typical manner of transporting altricial young prior to locomotor competence (Ewer, 1968). On three occasions young were placed in the pouch of the female (Earl, 1977); however, this is attributed to the female being agitated and is classed under displacement activity. On one occasion, a three week old pup attempted to climb into the mother's mouth, presumably after food. The only known case of pouching during retrieval occurs in Liomys, where a female may place a young in each of her two pouches (Eisenberg, 1963a). Initially, Saccostomus pups are picked up mostly by the neck area; as the pups get older the grip moves, in the majority of cases, towards the central dorsal surface (Table 1). Carlier and Noirot (1965) suggested that the transporting grip is improved with practise; another reason could be that as the pup becomes heavier and more active, the dorsal surface presents a bigger, and therefore easier area, to grip.

In the first few days post partum, a few females picked the pups up with the forepaws and placed them in the mouth. This type of behaviour was only observed till approximately the 4th day. During the first few days post partum the pups were hypersensitive to tactile stimuli and squirmed and jerked so extensively when the female attempted to grip them with her mouth, that frequently she was unable to do so. Picking up with the forepaws alleviates the above situation, as the young are initially held in a firmer grip and once the female has them gripped in her mouth, they tend to become more passive. Cricetomys (Ewer, 1967) was also seen to retrieve the young using the forepaws (but directly into the nest) when unable to pick them up in the mouth. A decrease in the jerking of the pups was attributed to a passing of the phase, and not an improvement of handling technique.

Normally the pup becomes still as soon as a female grips it. However, towards the end of the retrieval period the young were more independent and often did not want to be picked up, and would try to run away from the

Table 1. Body areas whereby young of *Saccostomus* are carried over a 22 day period (n = 73).

Surface gripped	Percentage of times
Dorsal surface	56,8
Back	47,0
Rump	9,8
Neck area	32,4
Extremeties	10,8
Tail	2,1
Head	0,7
Ears	0,3
Legs	7,7

female. As a result the female gripped whatever part of the body she could get hold of, with an increased number of grips on the extremeties, as indicated in Fig. 8 . Both ear and head grips only occurred after day 18. Prior to that the leg represented the majority of the extremeties which were gripped.

The overall retrieval time approximately a week post-partum increased rather than decreased as found by Carlier and Noirot (1965), mostly due to increased activity in the nest between successive retrievals (Fig. 9). There was a decrease in the total retrieval time after day 18, as at this stage the young started returning to the nest on their own. From day 16 to 17 some young would start following the female after she had retrieved one pup, and the female would then retrieve them half way to the nest. At about this time the impulse to retrieve started decreasing, especially in some females; the decrease in retrieval was compensated for by an increased exploratory urge in the young, and their increasing ability to return to the nest o their own. Decrease in retrieval motivation was also shown by the female merely mouthing the young, but not picking them up. This however, did not occur very regularly.

The latency period was the lowest during the first week or so post-partum (Fig. 10). During this time the motivation to retrieve is the strongest, and the female would rush out as soon as the young were placed in the cage. After the eighth day there was an increase in the latency period, and thereafter it fluctuated widely, as some females would go to retrieve instantly, and others took longer. Rowell (1961) observed an increase in the latency period in hamsters just prior to the sudden cessation to retrieve. Retrieval ceases gradually in

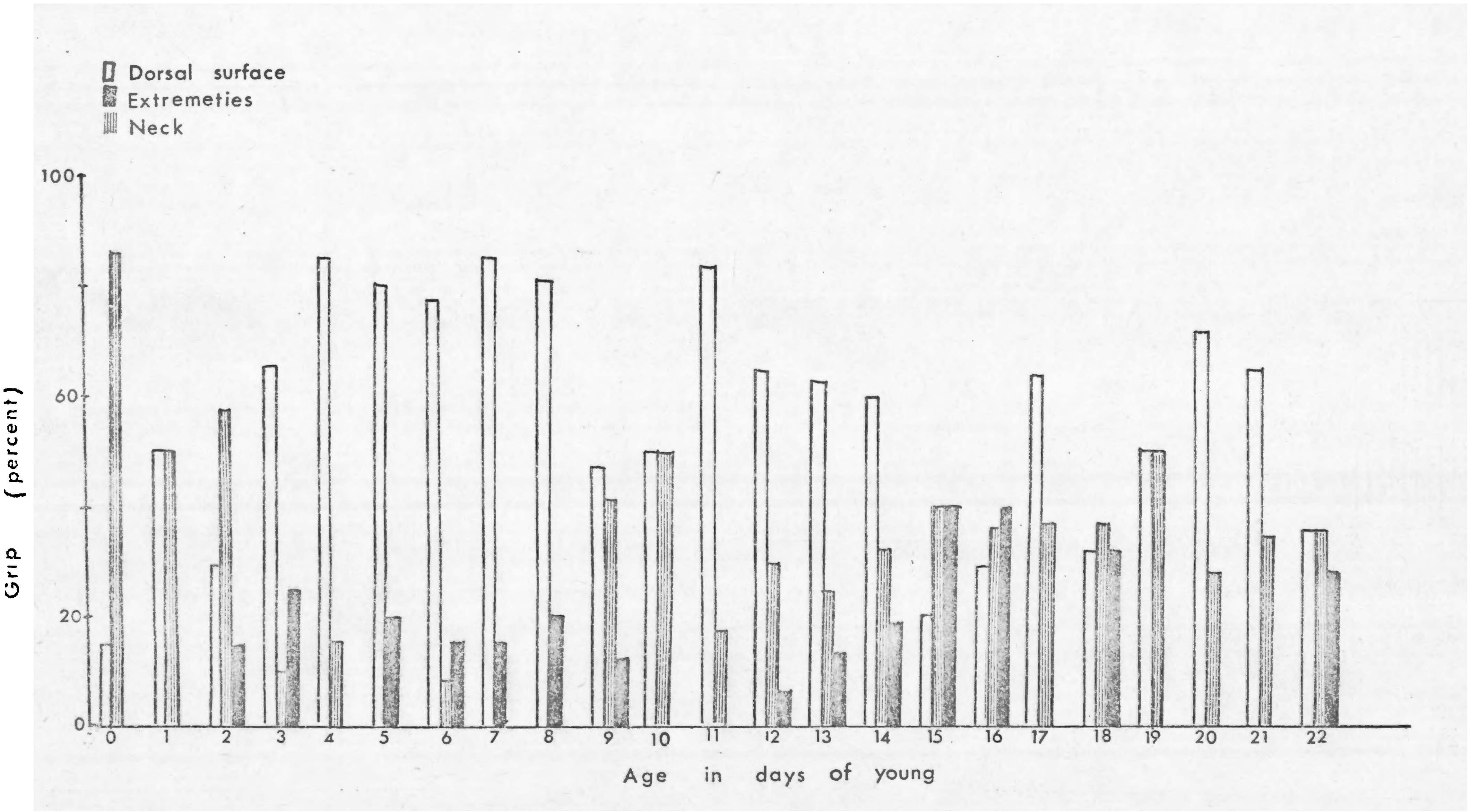

Fig.8 Manner of transporting young of *S. campestris* during retrieval (n = 73).

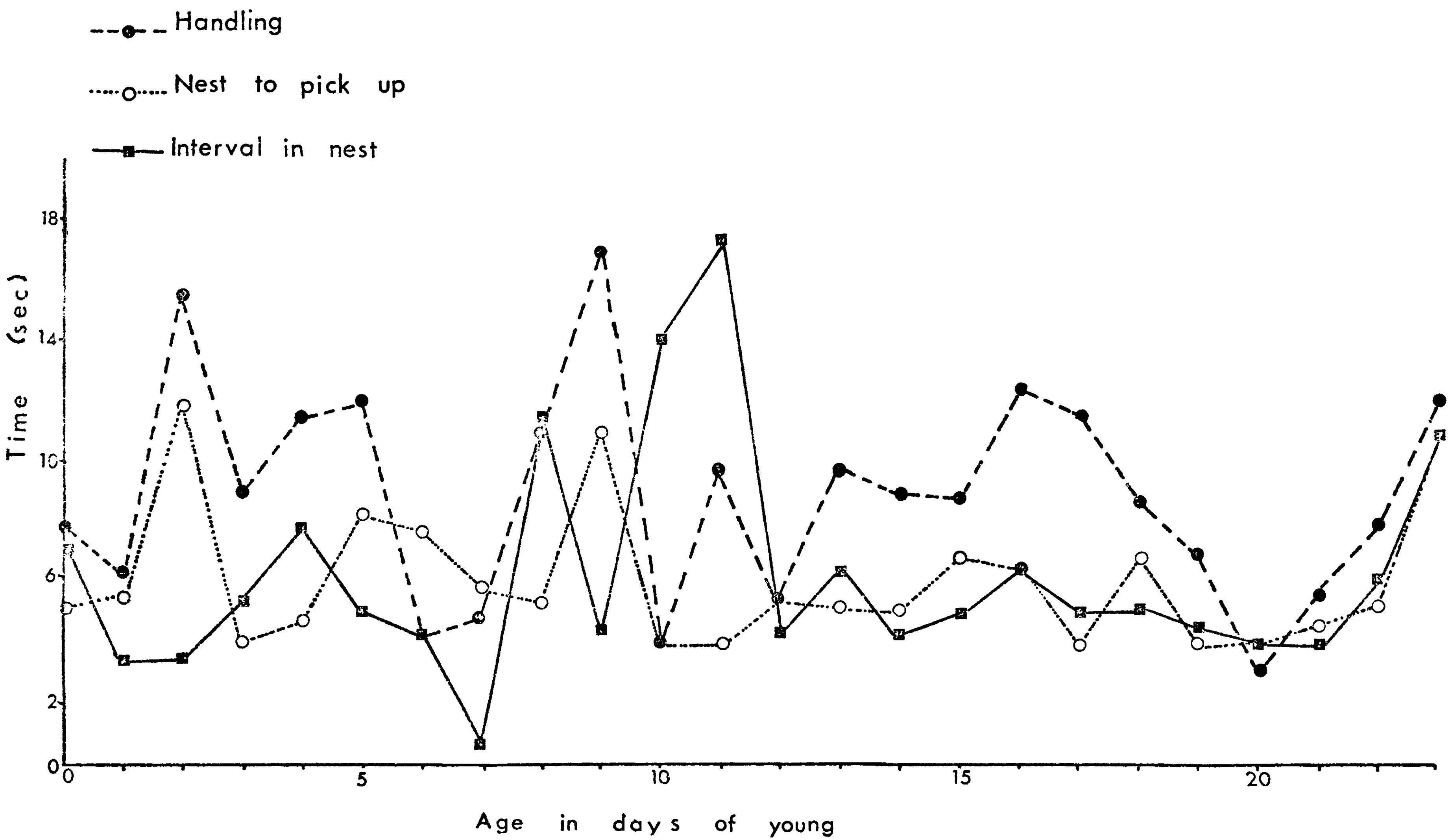

Fig.9 Time spent in handling young, interval in nest and time between leaving the nest and picking up successive young during retrieval in S. campestris (n = 73).

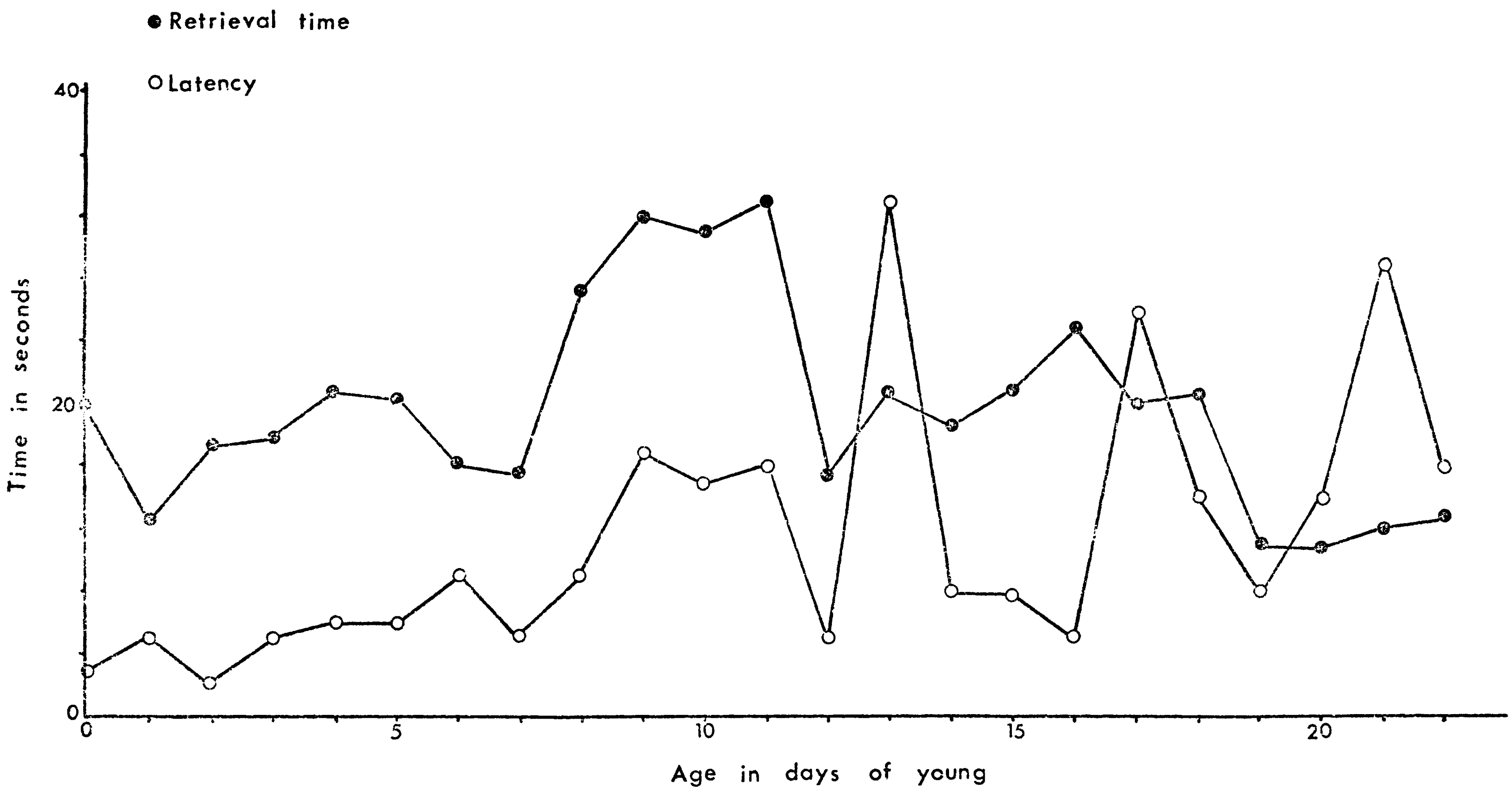

Fig. 10 Latency period prior to initial contact with young, and the mean retrieval time per young during retrieval in _S. campestris_ (n = 73).

Saccostomus, a decrease occurring from day 18 and retrieval stopping entirely on day 24.

Of the total retrieval time per pup, the longest time was spent in the actual handling of the young, i.e. from the first contact with the young till depositing it in the nest (Fig. 9). The time taken between leaving the nest and picking up a successive young was only slightly shorter than the interval in the nest.

Beach and Jaynes (1956 b), Carlier and Noirot (1965) and Michener (1971) all observed an improvement in retrieval with experience, mostly as a result of decreased latency period, decreased time spent on dispersed activities, and a more skillful handling of the pups. In Saccostomus the change in latency period cannot be used to indicate an improvement in retrieval, as the motivation to retrieve is the strongest post-partum, and as a result the latency period shows a general increase with increasing age of litter. An improvement in the handling of the young occurred after the first week, as reflected by the decreased number of grips per young and the amount of times each individual was picked up (Fig. 11). However, improvement in handling can also be attributed to increased passiveness in the young at this age. The time spent in the nest by the mother increased greatly during the second week post-partum. This may be attributed to a more intensive grooming of each young after retrieval.

However, one of the factors that indicated a greater confidence in the

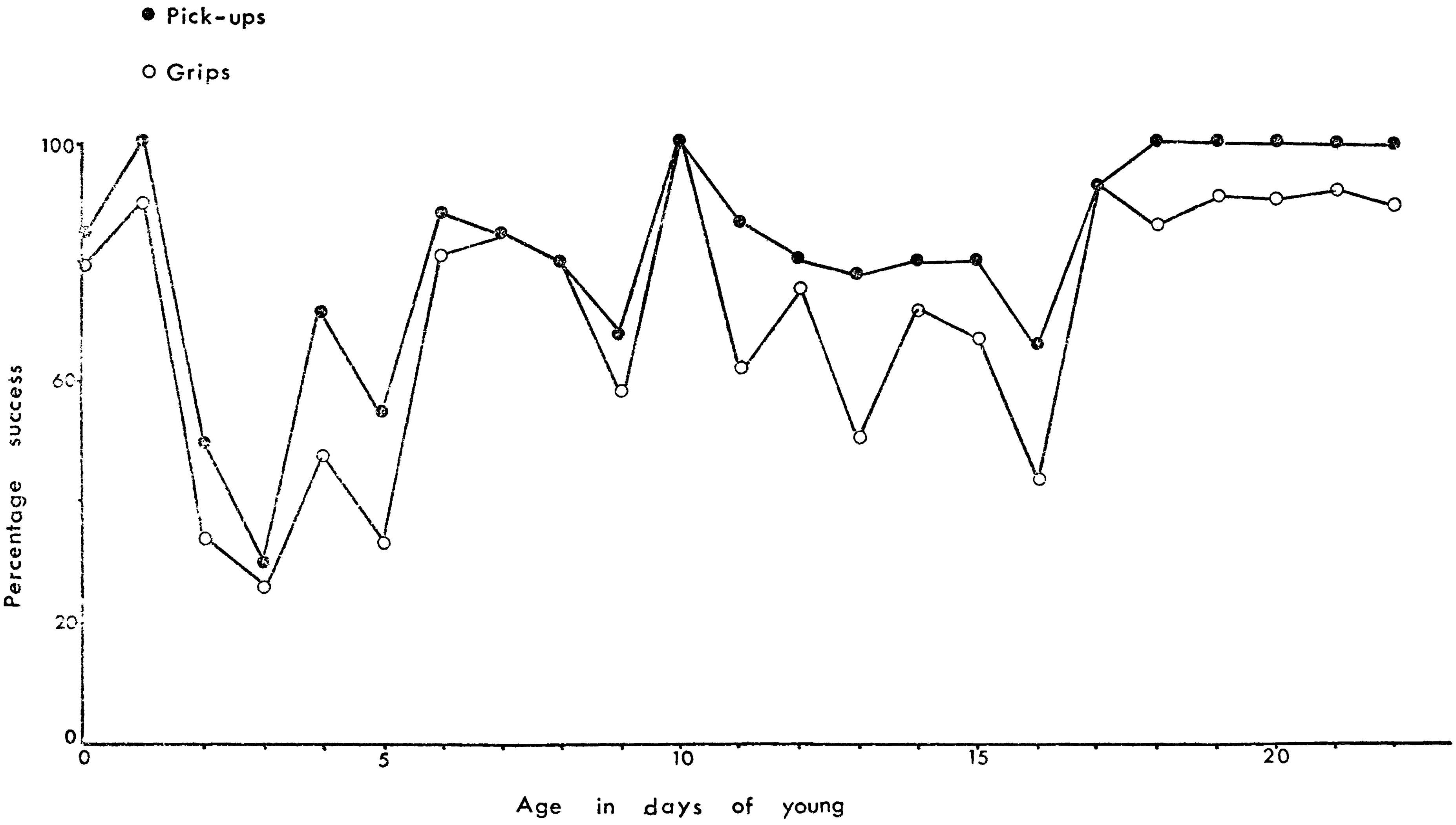

Fig. 11 Pick ups and grip changes (per cent) during retrieval by S. campestris.

mother during successive retrievals was the decrease in displacement activity, and also more successful retrievals (i.e. pick up). During the first few days after birth, sometimes for up to a week, the young would be extremely vocal when gripped. This caused the female to release them and she normally performed a few quick face wipes or a face wash, and would also return to the nest empty-handed. The female would always return to the nest if she had dropped the young while on her way there, thus showing the instinctive urge to finish off the retrieval sequence. Displacement activity in a form other than grooming, which was the most common, occurred with the female rushing around frantically with a pup in her mouth. In the same way food was sometimes pouched, and on two occasions live pups (Earl, 1977), whereafter the parent rushed around.

The route traversed between the pick-up site and the nest was always direct, apart from one female which retrieved all her young by a circular route, but only on the sixth day. No explanation for this deviation from the normal pattern was apparent. In the majority of cases the female left the nest after all the young had been retrieved to check if there were any left.

Stimuli initiating retrieval

Barnett (1963) observed that retrieval in the rat was a stereotyped form of behaviour in response to visual, chemical, tactile and vocal stimuli from the young, whereas Tinbergen (In Beach and Jaynes, 1956) noted that an instinctive reaction responds to very few stimuli. In Saccostomus it was found that any one of the above stimuli, or more than one, at a given time, could initiate the retrieving response.

Olfactory stimuli were found not to be essential for retrieval in Saccostomus, although on occasion, but not always, discrimination did occur between own and alien young. The same was observed by Beach and Jaynes (1956 b) for rats. Discrimination on olfactory grounds did usually tend to increase towards the end of the retrieval period, probably due to a decline in the strength of retrieving response. The alien young were always retrieved, and no attacks occurred.

Thermal stimuli are also not essential, although thermal discrimination was quite distinct, as dead and cold young were subjected to intensive investigation. However, these young were also retrieved, albeit only after all the live pups. It is not probable that these individuals were regarded as food, as was found to be the case with refrigerated young of rats (Beach and Jaynes, 1963) which were taken to a separate food corner. It was difficult to differentiate in Saccostomus as all food is stored in the nest. Food was only retrieved towards the end of the retrieval period; this can be at least partly attributed to the increased exploratory activity, which correspondingly increases the chances of finding food.

Vocal stimulation initiated retrieval in most cases, especially during the first ten days. However, on two occasions two different young sent out very distressful squeaks, one for 4½ minutes, the other for over 12 minutes, prior to being retrieved.

Visual and vocal cues appear to be the most important in initiating retrieval. All live and active pups were always retrieved prior to any dead pups, although the latter were still warm. In a few instances the female also attempted to retrieve her mate, or young from an older litter. They were, however, too heavy to carry.

In conclusion it can be stated that no single type of cue is essential for retrieval, but that various cues can evoke retrieval.

EPIMELETIC BEHAVIOUR

This is the care giving of the mother to her young and includes giving of warmth, grooming and protection. The young are sheltered and kept warm by the female's body and by the nest. The first few days post-partum the female rarely leaves the nest. Contactual behaviour is strong, ensuring that the young and mother stay together, as discussed under postnatal development.

Grooming of the young is frequent and thorough immediately post-partum. The genital region of the young is most frequently groomed, to promote elimination. After handling, the young were examined thoroughly, groomed, and pulled in under the female, presumably to facilitate nursing. Both male and female groom the young. At about four weeks of age, the young start grooming each other and the mother. After about 70 to 80 days, the 'juveniles' become intolerant of the female's attempts to groom them; allogrooming also diminishes and eventually ceases almost totally.

No increase in aggression was ever observed towards the handler before or after parturition. Conspecifics were usually, but not always, driven out of the nest a few days prior to parturition, and normally allowed to return to the nest three to seven days post-partum. On one occasion two females littered within three days of each other and nursed the litters in a communal nest. No protectiveness or increase in aggression was ever observed in the male.

As in Desmodillus (Keogh, 1973), maternal behaviour in Saccostomus is affected by the female's physiological state. If a mother became pregnant, toleration of her litter decreased, and she frequently became quite aggressive. However, if not pregnant, the female remained tolerant longer, even till the litter reached adulthood, provided the cage was not overcrowded.

The predominant social interaction between mother and young occurs during the neonatal (0 to 4 days) and the beginning of the transitional (5 to 16 days) periods. The young are totally dependent on the mother during the neonatal period. During the transitional period contact is still maintained, and the young remain in the nest. They start to become independent of their mother's food. After about three weeks there is only limited contact between parents and young for suckling and grooming; both diminish in frequency with increasing age till the late juvenile stage, when the young become intolerant of any further attempts of maternal care. Despite their increasing independence, it is probable that the female's behaviour during the transitional and juvenile period is important, as the young have been observed copying her. This was especially noticeable during digging and nesting.

Chapter 3. REPRODUCTION AND PARTURITION

REPRODUCTION

The gestation period of *Saccostomus* is 21 days (n = 5). The average duration between introduction of a male and production of a litter was 33 days. Litter sizes varied from a maximum of eight in two litters, to a minimum of two young, in five litters. The average litter size wa 4,9 with SD = 1,66. Keogh (*pers. comm.*) obtained an average litter size of 4,3, Pitchford and Visser (1970) an average of 6,0 with a range of 3 to 10. Smithers (1971) found an average number of 7,4 foetuses in pregnant females (n = 8) in Botswana with a range of 5 to 10, and an average of 6,7 in Rhodesia (*In Litt.*). The smaller litter size of captive *Saccostomus* (i.e. 4,9; 4,3 and 6,0 as opposed to 7,4 and 6,7) can be partially attributed to restricted laboratory conditions as discussed under Social behaviour. The sex ratio of newborn young (n = 80) was 0,543 males to one female. This did not differ significantly from a 1:1 ratio (x^2 = 0,51). De Wit (1972) also found no significant difference from a 1:1 sex ratio when trapping *Saccostomus* near Pretoria.

The minimum interval between litters was 24 days, which is the same as that found in *Praomys (Mastomys) natalensis* (Meester, 1960). The average littering interval between 1st and 2nd litters was 15,2? days (n = 13), 2nd and 3rd litters 72,6 days (n = 6) and 3rd and 4th litters 56 days (n = 2), showing a tendency for a decrease in littering interval between subsequent litters and increase in age of the female. The overall average littering interval was 83,3 days (n = 19). The wide variation in littering intervals was attributed to seasonal breeding. Keogh (pers. comm.) obtained 2,6 litters, and Pitchford and Visser (1970) 4 litters per breeding season, as opposed to the present study with a figure of 1,8. This was lower as the young were not weaned from the mother as soon as in the above cases, which resulted in decreased pregnancies.

The average age of the female at first litter was 130 days, with a rang of 67 to 292 days. It can be assumed that the minimal age at sexual maturity for females, allowing for a 21 day gestation period, was 46 days. As this case was a sibling mating, the same minimal age can be assumed for males. The age at which the first litter was produced depended on whether the age of sexual maturity was attained within the breeding season; if not, the animals only mated the following season. Measroch (1954) observed that female Tatera brantsi reached puberty at the age of either approximately 3 or 8 months, depending on factors stated above, and that no females of Tatera afra reached puberty during the anoestrous phase. The oldest recorded age at which a litter was produced by Saccostomus was 394 days.

Breeding was seasonal and occurred from August to March (Fig. 12), with only one litter being born in April. The largest number of litter was produced in January, with smaller peaks occurring in March, September and December. De Wit (1972) observed breeding in free-ranging Saccostomus from September to March. Smithers (1971) captured gravid females from January to April, and juveniles in September, October and February.

Breeding of Saccostomus could also be induced during winter if the temperature, photoperiod and relative humidity were increased, though

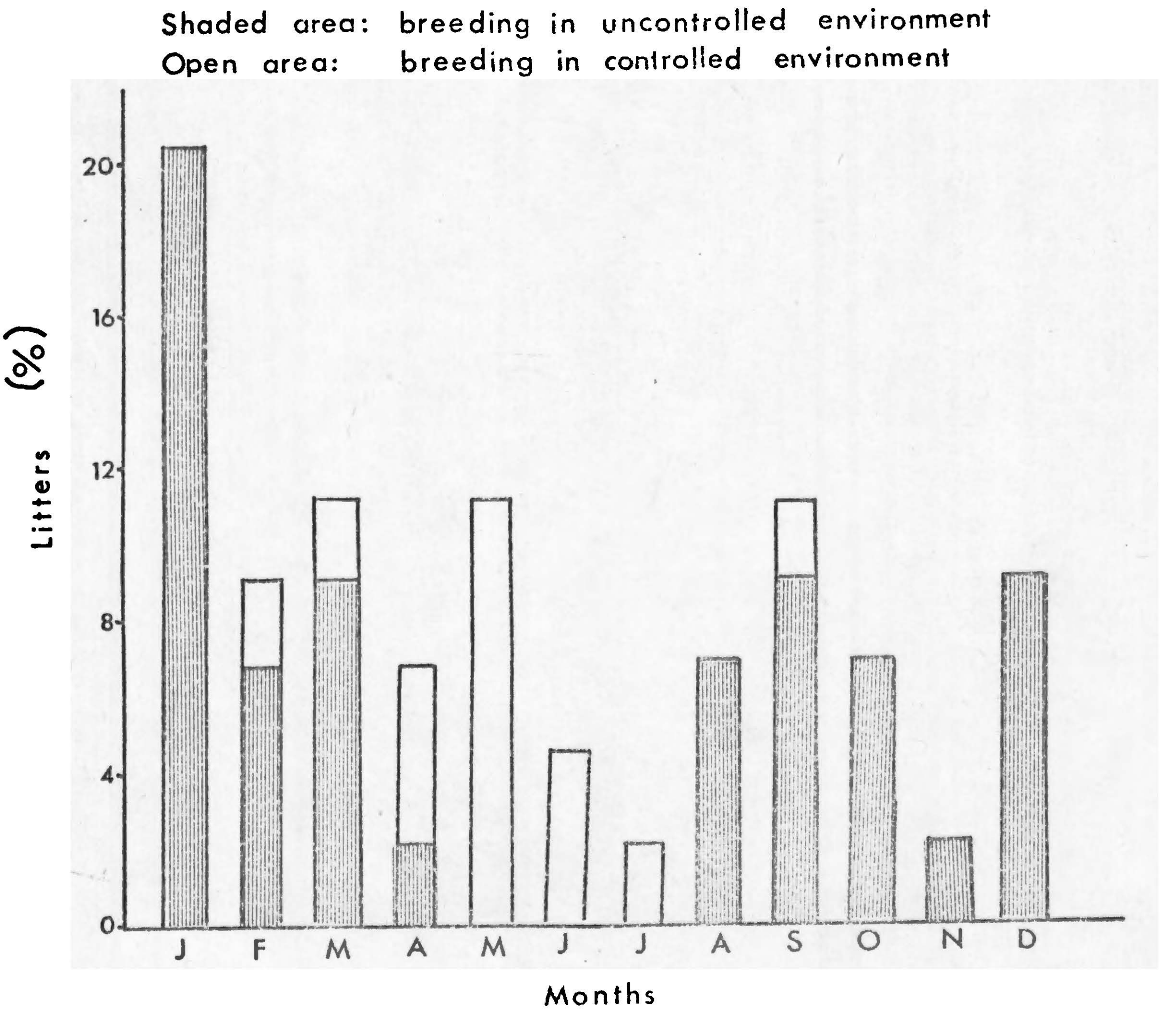

Fig 12 Breeding seasons of *S. campestris* based on birth of litters.

the former two factors were the more critical, (Fig. 12). Keogh (pers. comm.) who maintained a colony under semi-controlled conditions (temperature of approximately 24°C) observed peaks during August, September and December, with lower peaks in May, July and October. An increase in the photoperiod was also found to increase fecundity in Gerbillus paeba coombsi (Hallett and Keogh, 1971) and to induce fertility in Gerbillurus paeba paeba (Stutterheim and Skinner, 1973). The ability to increase fecundity by increasing the photoperiod and room temperature could be of advantage to the breeding of aseasonal breeders under laboratory conditions.

Dieterlen (1967) found that certain periods of low reproduction during the breeding season were caused by an actual phase of population increase. This factor could probably explain the peaks interspersed with low breeding figures, occurring also in Saccostomus within the breeding season. In the majority of littered females pregnancy within the breeding season was delayed until the litters were removed, irrespective of age post partum.

The young were separated from the mother at an average age of 83 days, with the earliest separation occurring at 41 days. In the majority of cases the young of parents in the rat breeding cages had to be removed as a result of female aggression. In larger cages, such as aquaria, young rarely were removed due to aggression, as they had more room to move and thus escape from the female. It is probable that wild adult Saccostomus chase their offspring away from the nest during this stage, which corresponds approximately with the attainment of sexual maturity of the young.

Of 16 recorded times of parturition, 14 occurred before 12h00, and nine of these between 06h00 and 10h00. The only birth that Wrangham (1969) recorded, occurred in the afternoon.

Average mass increase of a female during pregnancy was approximately 2,5 g during the 2nd quarter of pregnancy, 9,6 g during the third, and 15,3 during the last quarter. Total mass gain during pregnancy was around 28 g; 18 per cent of the increment being the mass of the young, excluding amnion and placenta. Dieterlen (1963) observed a 75:25 per cent mother young ratio in the body mass of <u>Acomys dimidiatus</u> at parturition. Female <u>Saccostomus</u> returned to their pre-pregnancy weight on average around the eighth day post-partum, though this varied between individuals. Most females appeared to fall below their pre-pregnancy mean body mass 3 weeks after parturition, and only regained their normal mass at approximately 40 days post partum.

PARTURITION

A few days prior to parturition, the female becomes increasingly aggressive; this usually serves to drive away her mate and other conspecifics. Alternately the male may be killed or seriously wounded. However, female aggression differed between individuals, and on several occasions the male was tolerated in the nest, and even allowed to 'help' the female throughout the birth process. When chased away, conspecifics usually returned to the nest a few days post-partum.

While giving birth, the female sits on her haunches so that the vaginal opening is directed anteriorly and the young are expelled forwards unde her own body. This posture is common to altricial rodents (Ewer, 1968) Delivery is fascilitated with the forepaws, and the neonate may also be pulled with the mouth. It appears that the young are born free of any restraining membranes; the afterbirth is expelled after the birth of the last young and eaten.

Each young, or part thereof, is cleaned as it appears, thus preventing the nest from becoming soiled. Once it has been expelled, the neonate is held in the forepaws and thoroughly groomed. Initially, licking does not necessarily follow the direction of the furpile as is later normal during grooming; the fur is licked in any direction, this presumably loosening the hairs and allowing all birth fluids to be licked away. Initial licking of the nasal region is essential to stimulate respiration (Ewer, 1968); the young were usually licked from the nose down. Stimulation of the anogenital region is also essential for defaecation and urination to take place, and is performed till after the young start leaving the nest. This behaviour is characteristic of altricial species (Ewer, 1968), and is important in maintaining nest cleanliness.

Between deliveries, the female constantly licks her genital area to remove birth fluids; this also prevents the nest from becoming soiled. Genital grooming is interspersed with grooming of the young. Keeping the nest clean is of utmost importance in Saccostomus, as they are nesters and burrow dwellers.

Young born dead are first groomed thoroughly, as if to start them breathing, then consumed. One male groomed a neonate for 4,08 min prior to eating it, which took 1,24 min.

It appears that no nursing occurs till after delivery of the afterbirth

The squeaking of the young immediately after birth can be caused by searching for nourishment. A female in an advanced stage of pregnancy was observed suckling newly born young of a conspecific female; this was also observed in the precocial Acomys (Ewer, 1968).

Following is an example of the times (seconds in parenthesis) of the birth of five young:

Birth (0);

contractions (334), birth of 2nd young, hindleg presentation (443);

contractions (596, 689, 789), birth of 3rd young, tail presentation (1020);

contractions (1361, 1412, 1426, 1614, 1685) birth of fourth young, dead (1739);

contractions (2021), birth of 5th young (2153);

delivery of afterbirth (2564)

suckling started (2955) or 49,25 min.

The mean time between deliveries was 7,05 min.; the actual birth of each young took approximately 50 s. The duration of contractions increases (from approximately 2 to 14 s) prior to the birth of each neonate. During a strong contraction the body is frequently extended.

Behaviour of the male during parturition

If the male was present, he was hyperactive and appeared restless; displacement activity was frequently observed. If the male was tolerated by the female within the nest, he took an active part in the birth. He sat close to or next to the female, and as each young was born, he would literally snatch it from out of the female's paws, and groom it thoroughly. This gave the female more time for self grooming. The male occasionally licked the female, and one male was observed eating the placenta. The male also retrieved young, placing them close to the mother's body; the female was tolerant of the male in this situation, and showed no aggression.

BREEDING IN CAPTIVITY

Saccostomus are not prolific breeders under laboratory conditions. It appears that the most important factor limiting breeding success was restricted space, or alternately overcrowding. In the larger cages the females were often either pregnant or lactating, whereas females in the smaller cages generally had longer periods between litters, unless a litter died at an early age. If two females were kept with one male, breeding in the subordinate female was usually restricted or totally absent. Eisenberg (1967) has noted that the female reproductive cycle is inhibited when a solitary species are forced to live paired in small cages.

Kirkpatrick and Valentine (1970) suggest the following factors which could contribute to nonbreeding in solitary type species under laboratory conditions: human disturbance, change in diet, restricted area of activity, and maintenance of the individuals in a social status not usual to them. The first two factors probably played no role in limited breeding of captive Saccostomus.

The maintenance of litter mates in pairs to reduce conflict was the primary method by which reproduction was enhanced although Eisenberg (1967) notes that in many typically solitary species this method was ineffectual. Alternately, if an adult male and female were placed together at the peak of the female's oestrous cycle, mating usually occurred. However, with this method timing is critical, and even then aggression was not always eliminated.

Chapter 4. ADULT BEHAVIOUR PATTERNS

MOTOR ACTIVITIES

Locomotion

Saccostomus is quadrapedal and walking and running is achieved by means of diagonal limb coordination; contralateral limbs are synchronised.

Walking appears to be the predominant form of locomotion. Running does not occur as frequently as in other rodents, and is much slower. Smithers (*pers. comm.*) has suggested that the 'sluggish' nature of these animals make them an easier prey for owls and other predators.

Head bobbing

Head bobbing occurs frequently in *Saccostomus*, although to a lesser extent in juveniles. It consists of a lifting and lowering movement of the head. Individuals are always stationary, and usually situated on a vantage point, i.e. on a rock, branch or nestbox. The ears are directed forwards, and the eyes wide open; the entire aspect of the animal suggests an investigatory state.

Head bobbing has also been observed in *Parotomys* (Nel and Rautenbach, 1974). Eibl-Eibesfeldt (1951) describes a similar or possibly the same type of behaviour and calls it scenting; the up and down movement is accompanied by sniffing and serves to take in air samples from different layers. It has also been suggested that head bobbing may serve to focus the eyes on a distant object.

As bobbing was only performed from vantage points it suggests a 'watchful' nature to this behaviour.

Stretching

Stretching sometimes occurs when the nest or nestbox is left on awakening. Stretching did not occur as frequently as it does in some other rodents (e.g. Davis, 1972; Stutterheim and Skinner, 1973 and Birkenstock and Nel, 1977).

Two types of stretching movements were observed in Saccostomus. During the normal stretching procedure, the limbs are extended alternately, and frequently one forepaw is raised. The back is dearched, so that the ventral surface of the body touches the substrate. The tail is arched upwards. The ears are laid back against the head and the eyes may be partially or totally closed. Stretching is usually accompanied by a large yawn (Fig. 13).

The diagonal stretch, whereby one forelimb and the opposing hind limb are extended, was also noted. However, in contrast to the normal stretching action which occurred on awakening, the diagonal stretch was seen as the animal walked about during foraging or exploring. It appears that the diagonal stretch was only performed when the individual felt safe and at ease in its own environment, and it could possibly serve to further relax the muscles.

Ewer (1967) suggests that the diagonal stretch is used when the animal moves along the burrows. The diagonal stretch also occurs in Cricetomys (Ewer, 1967), Gerbillus nanus

Fig. 13 Some postures of *S. campestris*: a) stretching; b) sleeping posture aloft; eating postures; c) food held in the fore paws, and d) food eaten from the ground.

(Kirschoffer, 1958) and the hamster Cricetus, all burrow dwellers; also in mice and rats (Eibl-Eibesfeldt, 1951).

Stretching was usually followed by exploration and foraging, and rarely by grooming, as observed in Peromyscus (Eisenberg, 1962).

Climbing

Although Saccostomus is not known to be arboreal, climbing occurred frequently if branches were provided. However, in this situation, climbing was mostly limited to males and juveniles, and it is possible they climbed to remain out of the females' immediate vicinity. Frequently a male or juvenile would escape into the branches when chased by a female; the latter rarely followed. Individuals, especially the adult males, would frequently spend a considerable time aloft. Grooming, eating (a pellet stored in the pouch) and sleeping aloft were common. Micturition and defaecetion also occurred while aloft.

In the holding cages, climbing of the steel bars of the cage lid was frequently resorted to by most individuals of both sexes. To start climbing, the bars are clasped with the forefeet and the body pulled up, enabling the hind feet to grip the bars. The tail was usually wrapped around the bar in a prehensile manner, as in Cricetulus (Lerwill, 1971) (Fig. 14). Individuals were able to hang suspended from the bars by the forefeet for several minutes.

Although Saccostomus is not adapted to climbing (Earl and Nel, 1976) it proved a capable climber; climbing ability improved with experience.

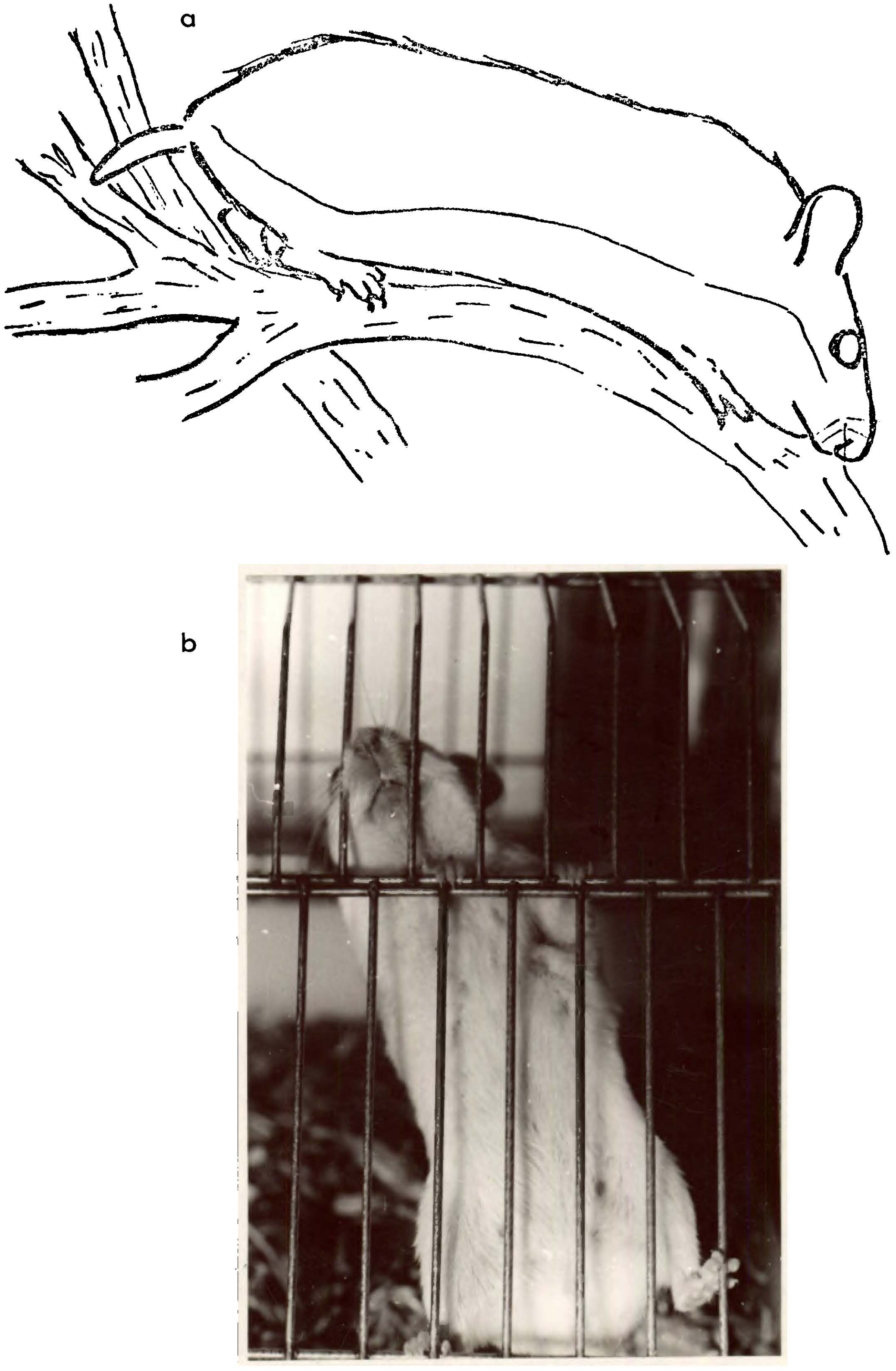

Fig. 14 Climbing in S. campestris a) on a branch and b) on the cage bars.

Saccostomus' climbing ability is largely due to the strong forefeet, and the use of the tail in a prehensile manner, which aids balance. The tail of Saccostomus, being short, is not adapted to climbing (Horner, in Layne, 1970), also no long tactile hairs which are characteristic of arboreal rodents (Herskovitz, 1969), are present. During climbing the feet are placed on the branch (Fig. 14).

The cliff edge response is an important indication of an animal's ability to climb (Eibl-Eibesfeldt, 1951). In juveniles, this response was poorly developed, indicating a lack of height discrimination.

It is probable that climbing in Saccostomus is largely an artifact of captivity. Climbing on the bars of the cage can be, at least partially attributed to boredom, and in some instances, for escape. In the cages with branches, climbing is largely attributed to the need for escape this is further supported by the females' almost total reluctance to climb

REST AND SLEEP

Rest

During rest one of several postures may be adopted. The hind limbs are lodged beneath the body, with the head either lying on the forepaws or resting on a littermate. This posture is also used during sleeping, and probably reflects a mood of utmost relaxation.

Another posture commonly used is as in sitting; the hind and forelimbs are placed beneath the body. Saccostomus frequently use this posture out of the nest, as compared with the first one which occurred only in the nest.

A few males and juveniles had favourite resting places in the branches, usually in a fork with the back quarters on and against one branch, while the forepaws rested on another. Females very seldom rested aloft

The animals liked to rest on an elevated position, from which they were able to observe their surroundings.

Sleep

Several postures are used for sleeping, but the most common, especiall in solitary individuals, was to curl up with the head and all four feet tucked in under the body. The weight of the animal rested partly on the hind feet and partly on the anterior dorsal surface of the head.

Two or more individuals together slept either curled up, (in the posture described above), side by side, or more usually with the head, and sometimes forequarters, on another individual.

Another posture adopted during sleep was lying on the side, with the body curved and the legs placed in front.

Occasionally, but only at high ambient temperatures, would Saccostomu lie stretched out, sometimes on their backs, with all four feet in the air, and the head stretched back or to the side. Heteromyids were also observed lying on their backs (Eisenberg, 1963). Body contact between animals was kept to a minimum when the temperature was high.

Body posture during sleep is thus dependent to a large extent on the number of animals sleeping together and the ambient temperature.

During sleep, some individuals would frequently twitch and jerk, and also vocalise, as if dreaming.

EXPLORATORY BEHAVIOUR

Exploratory behaviour is variously defined as "sensory inspection of the environment" (Scott, 1956) and "behaviour which serves to acquaint the animal with the topography of the surroundings included in the range" (Shillito, 1963).

Saccostomus regularly explores its home environment; this is accomplished mainly by sensory investigation of the terrain as the animal moves along, especially during daily foraging. No special posture is adopted during this type of exploration; 'scanning', as described below, may occur. Exploration in this way is contrary to the observations of Montgomery and Monkman (1955) who note that exploratory behaviour is evoked by novel stimuli, and not hunger, thirst, or general activity drives. However, Saccostomus ranges far during foraging (Smithers, 1971) and therefore continual exploration of the environment will ensure familiarity with the home range.

Exploratory behaviour is also elicited by a new environment, or a novel stimuli in an established environment. When investigating a new environment, the body is somewhat extended as the animal moves forward, or it may adopt this posture while remaining motionless and sniffing extensively. This is called the 'attend' posture (Fig. 15). In a few cases, when the individual was more afraid or cautious, the body was even more extended, so that the ventral surface touched the ground as the animal moved forward very slowly. The ears were

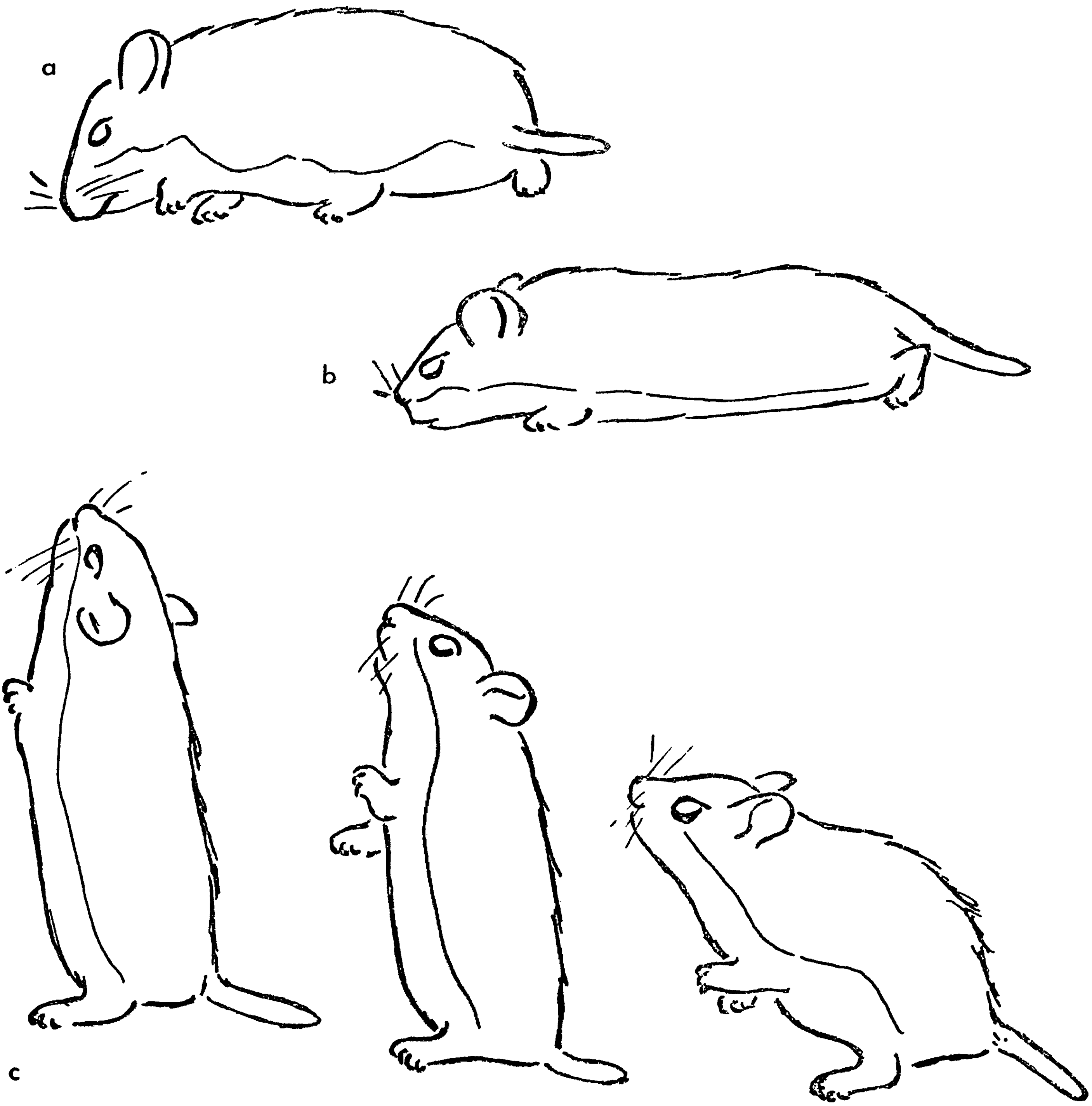

Fig. 15 Postures during exploration in *S. campestris*

a) 'attend' posture; b) 'slinking' posture, and

c) Scan, upright to semi-upright.

usually folded back slightly, possibly indicating fear (Fig. 15). However, this 'slinking' posture was seldom observed.

During initial exploration, movement is frequently interspersed with short periods of immobility, during which olfactory and visual investigation occurs. Alternatively, the animal may scan. During scanning, various degrees of the upright posture may be adopted, from the vertical upright (Fig. 15) to the near horizontal. Scanning presumably enables the individual to see for a greater distance. It is usually accompanied by whisker movement; the ears are erect and slightly forward, and the forepaws are held in front of the body.

During exploratory activity sandbathing, digging and pouching occur frequently. The ventral rub may also be performed, especially if a female is present. When the individual is placed in a new environment, exploration occurs immediately or within a few seconds of introduction. During initial exploration, activity was usually restricted to ground level; climbing only occurred once the environment was fully reconnoitred.

When a novel object was placed in the cage, it was usually investigated immediately; for instance when food was dropped into the cage, Saccostomus would literally rush up to investigate, showing no caution. Therefore, no 'new object reaction', or neophobia, as observed in wild rats (Barnett, 1958) and the vole, Microtus agrestis (Shillito, 1963), was ever observed in Saccostomus.

Lack of caution is further evidenced by total lack of any 'wall adhering tendencies', which commonly occur in many rodents (Davis, 1972 and

Shillito, 1973). This could partly be due to the preferred habitat of Saccostomus being rather open with little cover (although this does vary from area to area) if, as suggested by Brubaker (1968), wall seeking tendencies are indicative of a sheltered habitat. However, it is probable that this apparent lack of caution is due to Saccostomus' natural fearlessness; they seldom reacted to any loud noises, and when being investigated through the bars of their cage by cats, never ran away, but a bout of mutual investigation followed. Although their laboratory upbringing may have played some role in their docility, this was probably insignificant, as even newly caught wild individuals were unafraid, and could be handled immediately after capture.

During exploration, accumulation of sensory information is very important. This occurs initially by means of visual input, and is followed up by use of the tactile and olfactory senses (objects are nosed). It appears that auditory stimuli are the least important, as shown by the poor, or total lack of, any reaction to noise. To conclude, in Saccostomus exploratory behaviour serves two important functions; namely, acquiring information on the environment, and maintaining already existing knowledge of the environment. As noted by Barnett (1958) exploratory behaviour is important in adapting the individual to its environment; the reason why Saccostomus can survive in a variety of habitats may also be due to their extensive exploratory activities.

INGESTION

Diet

In captivity, Saccostomus will eat a wide variety of foods; Epol rat cubes, provided *ad. lib*. were supplemented with fruit and vegetables; sunflower seeds were particularly enjoyed.

In the wild, the diet includes grass seeds, as also seeds of *Acacia* spp *Grewia* spp. and *Combretum* spp. (Smithers, 1971). Roberts (1951) also reported the presence of termites in the cheek pouches.

Cannibalism occurred frequently in captivity. Apart from eating any dead or injured young, adults which were seriously injured and later died were always eaten, although to different degrees. Cannibalism usually started at the rectal area, then the stomach contents were eaten, as was found also in *Zelotomys woosnami* (Birkenstock and Nel, 1977). Frequently the skull was cracked and the contents eaten. Occasionally the lower legs, or part thereof, were eaten. Juveniles were frequently observed nibbling at the injured and raw backs or tail tips of the males.

On two occasions when no rat cubes were available, *Saccostomus* subsiste on a diet of fruit and vegetables. It appears that this was insufficient, as during both occasions cannibalism occurred, and it seems that the victims were killed solely for this purpose, as all individual were healthy and uninjured. Carnivory amongst rodents is not unknown; e.g. *Beamys major* (Hanney and Morris, 1962) although primarily vegetarian, is also omnivorous. Landry (1970) notes that some form of animal nutrition may be an important factor in rodent survival, and not merely an anomalous behaviour.

Coprophagy is common in juveniles, but was never observed in adults.

Eating of earth occurred at all ages, but sand was never eaten. The reason for this behaviour is unknown, but it could be to supplement some nutrient present in low quantity in the diet, although animals with no ground to eat showed no obvious signs of any deficiencies. Another possibility is an inherent liking for the taste of soil as during burrowing, earth was frequently transported in the pouches (see Burrowing).

Gnawing of bark occurred occasionally when twigs were provided. It is probable that this serves to sharpen the incisors, as does gnawing of the steel bars of the cage top. The latter habit was more common in certain individuals, and could be partly attributed to boredom. Eibl-Eibesfelt (1951) mentions that gnawing is an instinctive motor pattern for all rodents, and that shredding, which is not very common, has evolved from it.

Shredding (called chopping by Eisenberg, 1967) is the gnawing of food into small pieces, usually for stocking (Eibl-Eibesfelt, 1951). This behaviour is common in Saccostomus; usually all the rat cubes, irrespective of quantity, which were supplied in the trough of the cage lid, were shredded. If rat cubes were provided ad. lib., they were all shredded, till frequently the whole floor of the cage was covered, sometimes up to the lid (± 10 cm). Normally only food suitable for hoarding was shredded.

The behavioural components of feeding can be classified as follows: foraging, sniffing and sampling.

Barnett (1956) describes exploratory behaviour (foraging) as a major and highly significant component of feeding. During foraging, the animal moves along slowly, sifting and scratching, (occasionally digging, (see Digging, under burrowing)) with the forepaws. All food is stored in the pouch; if too large then it is gnawed into smaller bits and pouched, or else carried back to the nest between the incisors. Very small seeds, (e.g. millet) are possibly picked up by licking. Larger items such as vegetables and fruit are sometimes dragged back to the nest but more often immediately consumed. No 'new object' avoidance of food, such as commonly occurs in rats (Barnett, 1956) is present.

Eating occurred as follows: the animal sits upon its haunches with the tail stretched out behind, for balance (Fig. 13). A piece of food, if small enough to be manipulated, is picked up in the mouth. It is then grasped by the forepaws, and nibbled with the incisors. This way of eating commonly occurs in all rodents (Ewer, 1968). If the edible object is too large to be held, then the animal crouches over it, usually placing one, or both, forepaws on it and proceeds to eat by biting bits off (Fig. 12). If a larger morsel is pulled away, it is eaten in the manner first described.

Sunflower seeds are held in both forepaws. The seed is shelled by biting along the groove joining the two halves; the shell is then dropped and the contents eaten.

Feeding occurred mostly in the nest, as in Zelotomys (Birkenstock and Nel, 1977).

Feeding is normally followed by grooming, even though this may only consist of a quick paw licking and/or a face wipe, or else a more thorough groom.

Drinking

Water was provided ad. lib. in dispensers. To drink, Saccostomus stands underneath the bottle, either on all fours, or on the hind legs, with one or both borepaws gripping the neck of the bottle. Drinking is accomplished by licking the nozzle. Juicy foods, e.g. paw-paw, were also licked in this manner prior to eating.

When deprived of water for a few days, Saccostomus would rush to it eagerly when it was made available. However, as it is probable that their water supply is limited in the wild, it would seem that they drink more to satisfy a liking, than for any physiological need. In Gerbillurus (Stutterheim and Skinner, 1973), a rodent that can live without any free water, fighting occurred when they were deprived of it after having had a regular supply.

Pouching

Morphology of cheek pouches

Saccostomus possess internally opening cheek pouches, as also found in hamsters, heteromyids (Eisenberg, 1975), and some other rodents adapted to arid or semi arid environments; pouches are also present in Beamys and Cricetomys (Chiasson, 1954).

The pouches extend for approximately 35 mm from the corner of the mouth to well behind the ears on both sides, in the region of the shoulders. Immediately inside the pouch opening is a triangular patch, with its apex pointing rearwards, of specialised tissue sparsely covered with hair. The function of this patch is uncertain but some possibilities are suggested:

(i) that it is a gland secreting a digestive enzyme, similar to the parotid, submandibular or sublingual glands, which initiate the digestive process. (Food was frequently stored in the pouch for long periods).

(ii) that its secretion is used to mark the food (see Marking).

The pouches are capable of expanding to hold a large amount of food or other matter (Fig. 16). A female, in one minute, filled her pouch with 8,35 g of millet seeds. Another individual pouched 74 sunflower seeds (approximately 6,0 g) during one bout; compare this to Perognathus which normally pouches only two seeds (Bailey, 1939). Sunflower seeds are pouched, and hoarded, intact, and only shelled prior to eating. On one occasion a large rat cube (10 x 25 mm) was placed in one pouch, although some difficulty was encountered in manipulating it in and out. Masculature of the pouch is described by Chiasson (1954).

Method of pouching

During pouching seeds or other food matter are picked up directly in the mouth and pouched, presumably with the tongue, or pushed in with the forepaws. Pouching occurs either with the body in a horizontal position as the animal walks along foraging, or if the animal pouches during feeding, then pouching occurs in the feeding posture. The pouches are usually loaded alternately.

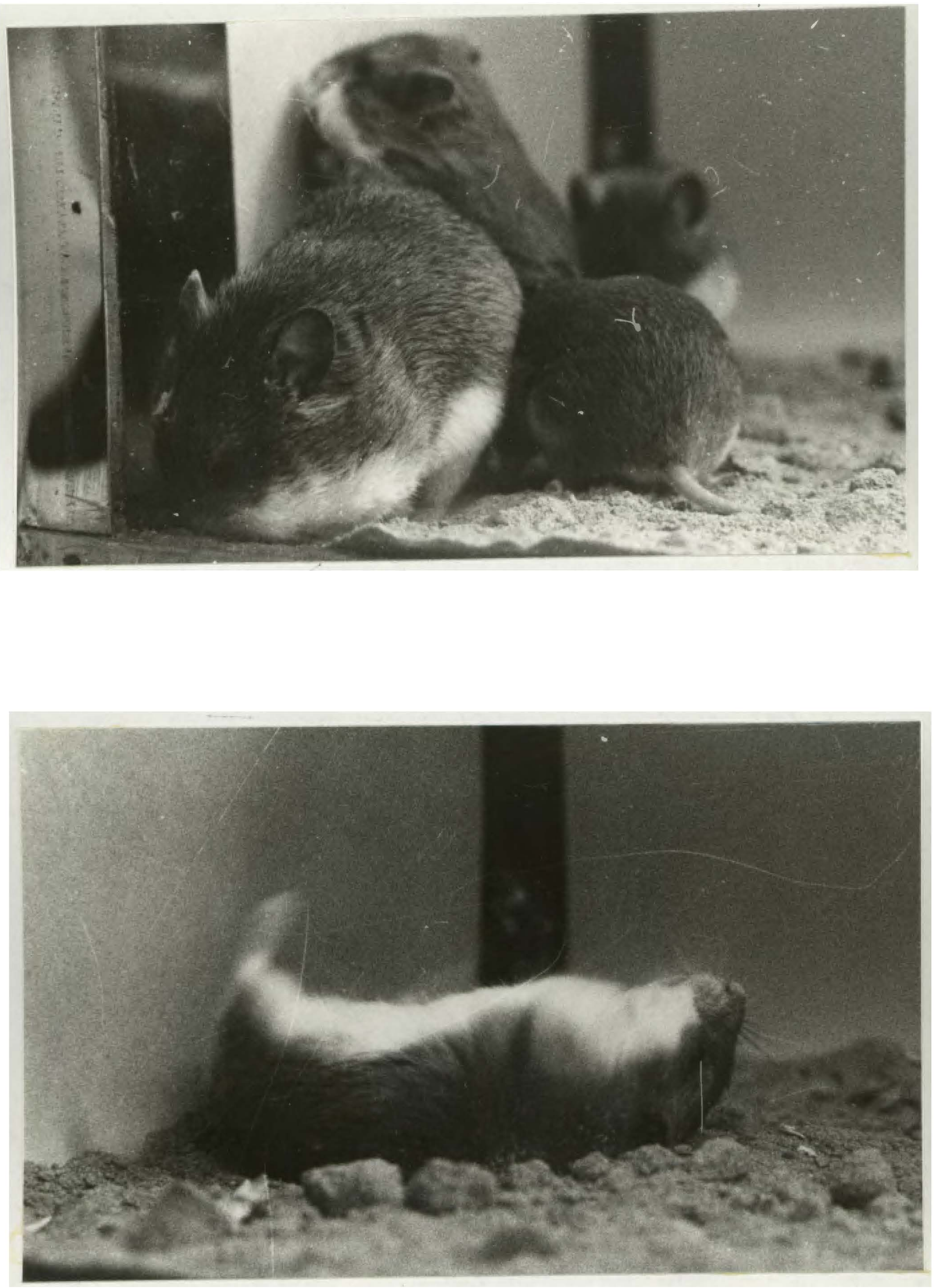

Fig. 16 a) Pouching (note expanded pouches) and b) sandbathing in *S. campestris*.

During unloading, the mouth is opened wide and the cheeks are pushed alternately with a sweeping action of the ipsilateral forepaw in an anterior direction. Occasionally, at the end of unloading when the mouth is still open wide, a muscle spasm occurs at the posterior end of the pouch, presumably to remove any matter which may be lodged there. The same manner of unloading was observed in the hamster (pers. obs. Eibl-Eibesfelt, 1951) and Perognathus (Bailey, 1939), as opposed to Cricetomys which makes infrequent use of the paws during pouching (Ewer, 1967).

Materials pouched

The majority of matter pouched was that collected for subsequent hoarding (see materials hoarded). Other items pouched included materials used in nest building, bits of stones, earth dug up during burrowing, nestlings (Earl, 1977) (see Retrieval), food for later eating at leisure, and also for hiding the food.

The pouch was usually only half-filled. However, when a favoured food, e.g. suhflower seeds, was available, the amount pouched increased dramatically.

Functions of pouching

Primary function is that of hoarding, as discussed later.

Transport, as during burrowing.

Hiding of food. Pouching, especially of favoured foods, frequently occurred to prevent another individual from getting it. Such an item was immediately pouched when a conspecific approached, to be later eaten alone, and in safety. This type of behaviour was termed food env by Ewer (1968). Juveniles especially were susceptible to food envy, frequently scrabbling over choice items and running to eat these in isolation. In one instance, a brick with a hole (approximately 35 mm i diameter) was placed against the side of the cage; the young repeatedly ran to this hole with choicy morsels, thus foiling the attempts by others to take it. Ewer (1968) suggests that, in *Xerus*, hoarding probably originated from food envy.

Storage. Food was frequently stored in the pouch to be eaten later at leisure. The normal daily activities, including drinking, were frequently performed with pouches filled.

Feed young. On a few occasions young were seen nibbling at bits of food in the mother's mouth; this food had previously been pouched. The food could have been partially digested, as stated earlier, and thus facilitated digestion by the young, and at the same time served to introduce them to solids.

In conflict situations (see Displacement Activity).

Pouching is advantageous to *Saccostomus* as a species, as it is a forager, gathering food matter into its pouches during its nightly explorations.

Hoarding

Ewer (1967) presents a very comprehensive discussion on hoarding. The term 'larder hoarding' refers to the storage of food within the animal's home. It is frequently encountered in species dwelling in burrows. 'Scatter hoarding' refers to general food storage where the food is usually dispersed and buried in seperate caches.

Saccostomus are larder hoarders. Scattering of rat cubes did occur, but appears to be an artifact of captivity. No specific pattern was present; it was probably the result of Saccostomus' habit of shredding all the available food pellets, and as there was no more room in the nest, the pellets were left lying all over the cage. This is not regarded as scatter hoarding.

Food for hoarding is usually transported in the pouch, although larger pellets may be carried in the mouth. Alternatively, both method may be employed simultaneously. The food is buried beneath the nesting material, and, if extensive, further scattered around the periphery of the nest. Beamys major (Hanney and Morris, 1962; Morris, 1962 and 1963) and Cricetomys (Morris, 1962 and 1963) also store food under the nesting material. The pouch is unloaded either with the snout pushed under the nesting material, or else near it, and then the latter is pulled over the food with the incisors, or levered with the snout to cover the larder. A pellet may also be pushed further under the nest with the snout. The larder is frequently partially exposed on the periphery of the nest. Some rodents (Bailey, 1939; Keogh, 1973) bury the larder by kicking sand over it; this was absent in S. campestris.

Materials hoarded

Saccostomus usually only hoarded rat pellets and seeds, or hard foods;

vegetables and fruit, or other soft food items, were rarely hoarded. On the few occasions that soft foods were taken to the nest, they were never placed under the nesting material with the rest of the larder. A female with young that was liberally supplied with soft foods, only took it to the nest when the young were 14 days old, and therefore old enough to start on solids. Ewer (1967) observed in lactating Cricetomys that the type of food hoarded was related to the needs of the offspring, and what was edible for them at that specific time.

The size of the rat pellets did not influence hoarding, for the larger ones were shredded. Large particles of food were rarely found in the larder.

Factors influencing hoarding

Amount of food available. Food collecting is independent of the amount of food available, although the amount actually hoarded was limited by the nest size.

Food type. Preference is given to certain preferred food types, i.e. sunflower seeds over rat pellets. Of five seed types, Saccostomus showed a great preference for peanuts and sunflower seeds (Pettifer and Nel, 1977). Further tests in the wild, or cafeteria experiments, are required to see whether the scarcer food types are given preference during hoarding.

State of security. Bindra (1948) states that hoarding in rats is dependent on their state of security; if no nesting cage was present, no hoarding occurred. This factor does not influence hoarding in

Saccostomus to any noticeable degree. Adults would frequently pouch almost immediately upon being placed in a new environment, even before selecting a nesting site. Thereafter, they would run around trying to find a suitable place to deposit the food. The difference in behaviour probably results from the rat not being a true hoarder. Bindra (1948) also noticed that shy animals tend to hoard more, thus allowing them to eat in the security of the nest. Juveniles also preferred to eat in the nest, but this was not classed as hoarding.

Hunger. Hoarding is not dependent on hunger, although satiation of hunger would appear to have a facilitatory effect on hoarding. If very hungry, Saccostomus would first eat, and only then commence to hoard, as was also observed by Pettifer and Nel (1977), who also noted that excessive starvation appeared to inhibit hoarding. The same situation is true in many other rodents (Morris, 1962; Ewer, 1967, 1968; Pettifer and Nel, 1977), although in Microtus hoarding was increased by hunger (Lainer, Estep and Dewsbury, 1974).

Functions of hoarding

Safety in the nest, as suggested by Bindra (1948), who stated that hoarding originated from the animals' need to eat in a safe and familiar place. This was evident especially in juveniles which frequently interrupted their activity to pick up a pellet, drop it in the nest, and run out again. Very young individuals frequently carried one pellet back to the nest for the specific purpose of eating it. Adults ate more in the nest, as already mentioned, but this was due to the availability of food in the nest. Petiffer and Nel (1977) observed that individuals only ate outside after prolonged starvation.

Provision of food out of season. This is an important function as many larder hoarders live in an arid/semi-arid environment, and are therefore for the most part dependent on seasonal foods. Dipodids (Eisenberg, 1975) have, however, a reduced hoarding tendency which is compensated by their capacity for hibernation or torpidity.

The early introduction of young to solid food, which is already present in the nest, as compared to non-hoarding species, where the young usually have to leave the nest prior to eating solids.

It can therefore be concluded that feeding, whether in the nest or not, and hoarding, are not motivated by the same factors; the latter serves as a storage against times when food is not readily available, while the former is chiefly dependent on hunger. Eating in the nest, especially in the juveniles, is accompanied by a greater feeling of safety.

Morris (1962) also stated that larder hoarding developed from the habit of taking the food into the nest to eat in safety; this of course would be more applicable to tunnel dwellers, e.g. Parotomys brantsii (Nel and Rautenbach, 1974) frequently took their food and ate near the entrance to the burrows, therefore hoarding could have evolved from further entrance. Dipodomys ingens, a scatter hoarder (Shaw, 1934) can be described as an intermediate form having larders both on the surface and within the burrows. It is a very efficient poucher, filling both pouches by a simultaneous 'shovelling' action of the forepaws.

Many rodents that practise larder hoarding are arid or semi-arid forms, tunnel dwellers, and also have the added advantage of possessing pouches. Hoarding, among other factors, is essential for survival in rodents adapted to arid environments. Hoarding instinct is so high in Dipodomys, the gaint kangaroo rat, that when dropped in a new environment, they start to pouch, prior to any other activity. Although to a lesser degree, this is also true of Saccostomus, thus emphasising the important part pouching, and hoarding, plays in the daily behavioural repertoire.

The type of hoarding, whether scatter or larder, is possibly determined among other factors, by the diet. Seed eaters, or those rodents predominantly utilising hard foods, appear to larder hoard in tunnels, whereas those which make primary use of soft foods, appear to scatter hoard on the surface. The advantage would be that soft foods could become mouldy in the warmer and more humid atmosphere of the burrow, especially when it is plugged, as most of them are. A good example is provided by Dipodomys (Shaw, 1934) which hoard green plant matter in surface 'pits', where it can be cured by the sun; later this matter is transported into underground larders. Saccostomus, which only larder hoard, differentiate between food types and only hoard hard food

ELIMINATION

Urination and defaecation take place in specific areas, which may overlap. These areas are usually situated in a corner or against the sides of the cage, outside the nesting area (Table 2 and Fig. 17). This could imply that in the wild defaecation occurs within the tunnel, possibly in a specific chamber.

Table 2 Position of nesting sites in cages, in relation to position of elimination sites (figures in per cent)

	Animals		
	males (102)	females (64)	pairs (8)
Opposite corners	31,4	34,4	25
Same side	65,7	54,7	62,5
Same corner	2,9	7,8	12,5

MALES (n = 31)

8		14
10	9	7
54	6	67

NESTS (n = 175)

29	1	24
8		2
34		25

ELIMINATION SITES (n = 123)

FEMALES (n = 24)

14	2	7
7	5	8
44	5	27

NESTS (n = 146)

28	3	13
1		1
14	1	8

ELIMINATION SITES (n = 69)

Fig. 17 Position of nests and elimination sites within the cages of *S. campestris*. (Each cage (represented by dark line) is divided into nine sections; numbers in each section represent number of nests or elimination sites).

Faecal pellets were frequently scattered throughout the cage due to digging, or sometimes fighting.

When about to defaecate, an animal would approach the site, sniff at it, and then turn around so that the hind quarters were situated over the heap. During defaecation the tail was raised and the hind legs extended, so that the hind quarters were raised slightly above normal posture. The ears were laid back and the eyes partially closed. The animal remains motionless till finished. Urination occurs in similar fashion.

Occasionally, after elimination, a few kicks with the hind legs occurred, as if to bury the urine/faeces. Eisenberg (1963) observed the same post-urination behaviour in heteromyids.

In some species, the placing of faecal pellets in specific heaps is of value in marking and communication. In <u>Saccostomus</u> this is unlikely as elimination probably takes place within the burrows and therefore conspecifics would not come into contact with the elimination sites.

GROOMING

Grooming occurred frequently and is an integral part of the daily behavioural repertoire. Grooming appears to be internally motivated, as noted by Barnett (1963) and Ewer (1967), although it may also be elicited by external factors such as wet fur, dirt or ectoparasites. I juveniles it is of shorter duration than in adults, as sequences are shorter, and grooming is also frequently interrupted by play.

Grooming involves the mouth (tongue and teeth), the forepaws and the hind feet (Fig. 18), as well as sandbathing. It consists of the following:

Lick paw The posture assumed may either be the usual grooming posture (Fig. 19) where the animal sits upright on its haunches, with the tail stretched out behind, usually helping to balance the individual; alternately, if paw licking occurs during displacement activity, the individual is usually in a more horizontal position. In the latter situation paw licking is incomplete and consists of just a few quick licks, which may or may not be followed by equally rapid face wipes.

Paw licking during a grooming bout is usually intensive and is followed, and/or interspersed, by face washing. The licked surface, on the inside of the paw, is used to clean the facial area. The area cleaned by the forepaws is represented in Fig. 18.

Face wash The posture during face washing is as for paw licking. Face washing is always preceded by licking of the paws, which is repeated continuously in order to keep the fur on the paw surface moist. During face washing the vibrissae, entire facial region and part of the head behind the ears are groomed (Fig. 18).

Initially, wiping starts from the snout region, subsequently proceeding further up the face, till the ears are included. During cleaning the ears are pushed forward and down as the paws pass over them. The meatus is cleaned by scratching with the toes of the hind leg. Face washing consists of a simultaneous sweeping movement of both forepaws, whereby the inner licked surface of the paws grooms the fur.

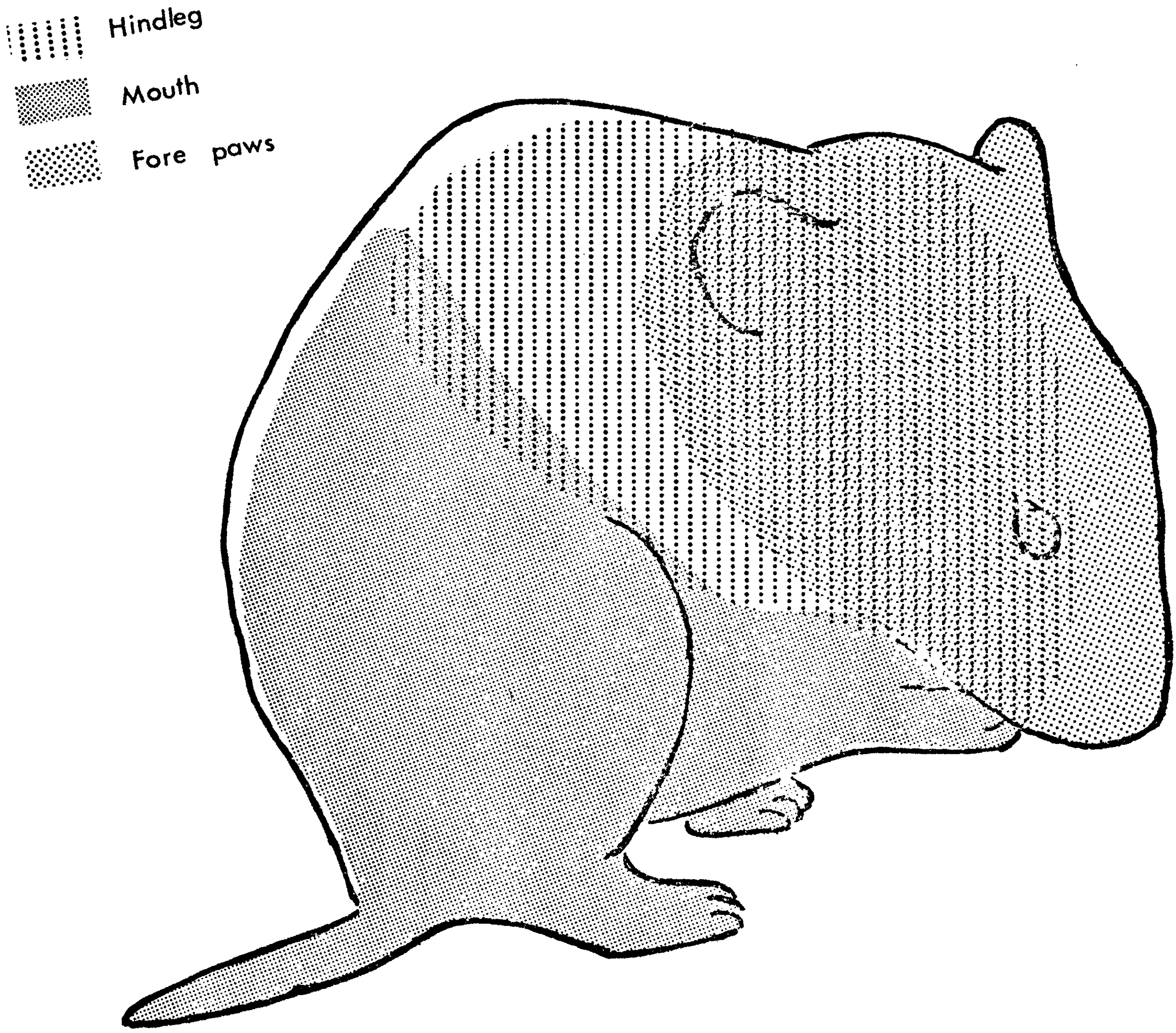

Fig. 18 Body areas groomed by the mouth, forepaws and hindlegs of *S. campestris*.

Fig. 19 Grooming postures of S. campestris: a) lick-paw, as during displacement activity; b) and c) lick-paws, as prior to face washing; d) face wash; e) and f) grooming of hind quarters.

Sometimes, during a face washing sequence, particular attention is paid to the pouch. The paw is rubbed vigorously over the pouch, pushing and pulling at the skin. This may be accompanied by the specific movement for totally emptying the pouch (see pouching). Contrary to face washing, washing of the pouch is usually one sided, or performed alternately.

The posture during lick paws and face wash remains unchanged, thus facilitating an uninterupted movement from one to the other.

Care of the body surface Grooming of the body is accomplished by hind foot grooming and scratching as described below, and by licking with the tongue. The latter is accompanied by nibbling at the fur with the incisors (mouthing), and a combing action whereby the forepaw, on the ipsilateral side, moves over the fur (Fig. 19f). The toes are spread, thus enabling combing over a wider area. The forepaw is also used to pull at the fur to facilitate licking. Licking, as observed by Meester (1960) always followed the direction of the fur pile.

Murray (quoted by Eisenberg, 1966) suggests that mouthing serves to remove ectoparasites. This is probable if the animal has ectoparasites but as none were present in Saccostomus, it can be concluded that mouthing is an integral part of the body grooming sequence, and as such is not dependent on the presence of parasites.

Postures during body grooming vary, depending on which cleaning agent is used, and which body part is being cleaned. When the body surface is being licked, the animal sits on its haunches and twists the torso around to the appropriate side. Both forepaws are off the ground, with the one on the side being licked usually holding, or against the fur. The ears are pressed back, or partially folded back against the head. When the body is being scratched or scratch-licked, the animal stands on both forefeet, and the hind foot not in use.

The abdominal and ventral surface of the body is groomed with the mouth; the sides, flanks, and part of the dorsal surface with a combination of mouth and hind leg, and the forequarter and front ventral area with the hindleg (Fig. 18).

<u>Grooming with/of the hind leg</u> Hind leg grooming consists of two units: grooming with the hind leg and grooming of the hind leg.

Hind leg grooming employs both the above units. Scratching of the body with the hind leg on the ipsilateral side, is interspersed with frequent licking and/or mouthing of the toes and claws. The latter serves to remove any particles of dirt, or in the wild, ectoparasites (Eisenberg, 1962), which become lodged under the claws during scratching. For a more thorough clean, the hind leg is held by one or both forepaws while being cleaned. The toes are spread to facilitate grooming in between. During hind leg grooming the animal sits on the posterior region of its back, and brings the hind leg right up to the mouth. The head is bent slightly towards the leg. A similar posture is adopted during tail grooming.

Scratching also occurs as a grooming entity, without the cleaning of the hind leg. Scratching bouts are usually out of the context of a grooming bout, occuring on their own without any other type of grooming activity. Scratching includes the head, neck, throat (the head is twisted up and away from the scratching foot); side and back as far as the leg can reach (Fig. 18). During scratching of the facial region, particular attention is paid to the meatus and inside of the pinna, and to the eye.

Tail grooming Grooming of the tail occurs infrequently. It never occurred as an isolated action, but most frequently followed grooming (licking) of the lower ventral area and the genitals. The posture adopted during grooming of the latter areas is maintained or shifted only slightly. The tail is grasped by the forepaws, the head brought forward and down, and the tail is licked along its length, starting at the base and proceeding to the tip, the head moves along as the tail is mouthed or licked.

Tail grooming occurs sporadically, and is less important than in other rodents. The tail is short and sparsely haired, and never trailed along the ground, therefore it probably does not get very dirty. Tail grooming is predominantly a male activity; probably to nurse injuries on the tails (see aggression).

Genital grooming The genitals are groomed entirely by licking. The animal sits on the posterior dorsal surface, as during hind leg and tail grooming, or on its haunches, with the body arched over. In the male, the penis is extruded and then held in the forepaws, while being thoroughly licked. Genital grooming is predominantly a male activity (Fig. 20 grooming during sexual encounters not included).

SANDBATHING

Sandbathing was common, especially after transfer to a new cage with

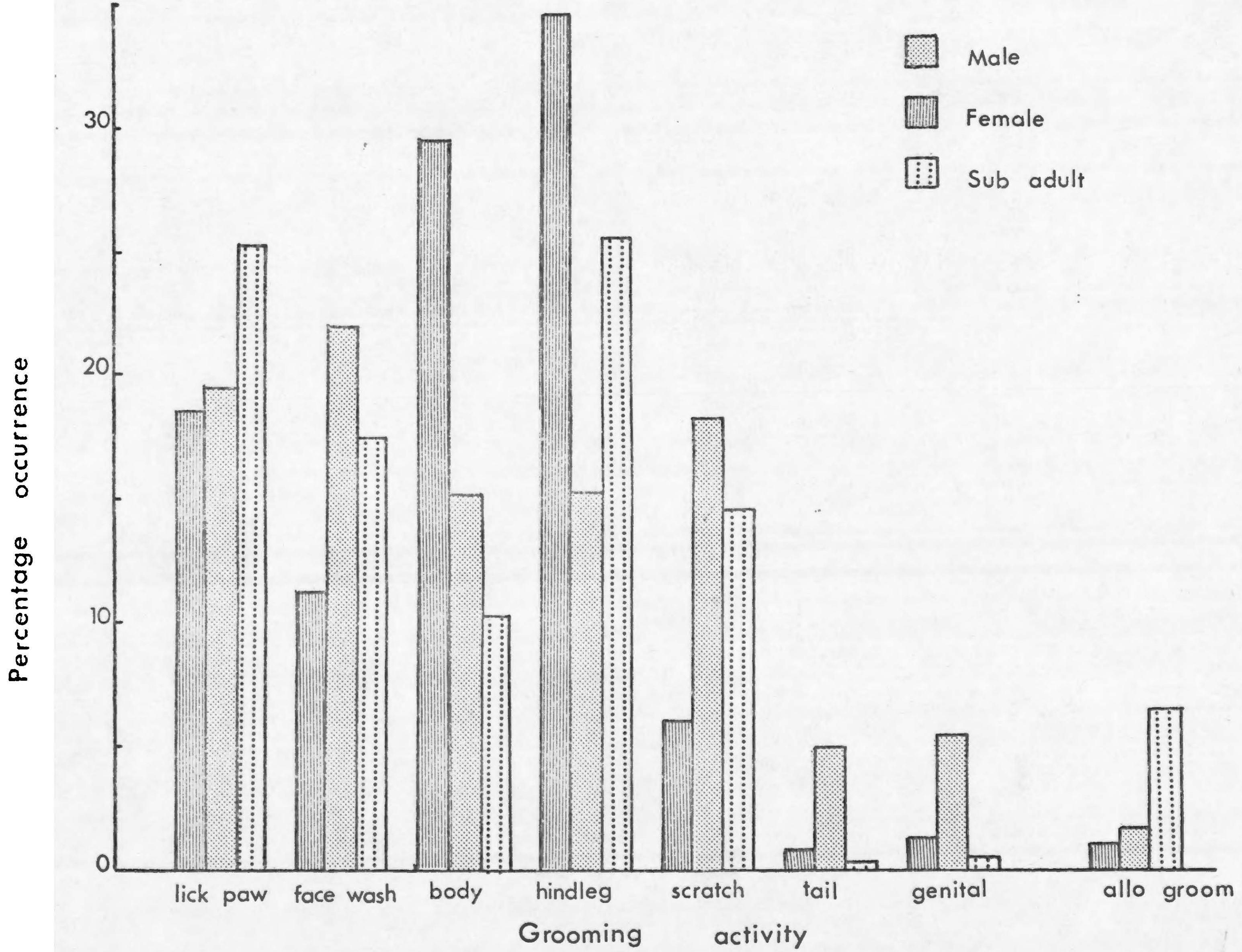

Fig. 20 Grooming activity of male (n = 8), female (n = 8) and juvenile (n = 13) *S. campestris.*

clean sand. Sandbathing in this situation was more prevalent in males, which sandbathed 47 percent of the time (range 30 - 60 percent) as compared to the female figure of 38,6 percent (range 26 - 50 percent)

A typical sandbathing sequence in Saccostomus is as follows: an individual digs a few times in the substrate, usually with the forefeet only to loosen the soil, and so dust the ventral fur. This is important in Saccostomus where the ventral rub is absent.

After digging the animal rolls over and performs a 'side-rub'. In Saccostomus the side-rub consists of a few writhes or shakes of the body against the substrate (Fig. 16). This is unlike the flexion and extension movement which Eisenberg (1963, 1967) describes for Heteromyidae. Duration of a side-rub varied, but it usually lasted only a few seconds.

During sandbathing the animals roll over partially, but not totally, onto the dorsal surface. Only a few rodents have been observed rolling directly onto the back, among them Tatera indica, Meriones unguiculatus and Pachyuromys duprassi (Eisenberg, 1967).

The right side was rubbed first in the majority of sandbathing sequences, especially in the female (Table 3).

During sandbathing the animal may perform between one and five side rubs, usually one or two (Table 4), on the same or alternate sides. Individuals never rolled over via the back, but would roll back onto their feet, then over onto the other side. Consecutive side rubs were infrequent, but when they did occur it was most often in juveniles (Tables 3 and 4), and never in females.

Table 3 Percentage of side rubs performed during sandbathing in *S. campestris*. (Alternate (1 to 5) and consequtive (SS) side rubs are presented as a percentage of the total number of side rubs of each respective side).

	Total no. (percentage) of side rubs													
	Right side							Left side						
	Total	1	2	3	4	5	SS	Total	1	2	3	4	5	SS
female	73	27	41	18	14			27	38	62				
male	58	33	20	33	7		7	42	36	27	27	10		
juvenile	54	28	34	28			10	46	31	35	14	5	10	5

Table 4 Percentage of total side rubs performed during sandbathing in S. campestris

	Total no. of side rubs					
	alternate					consecutive
	1	2	3	4	5	
female	30	47	13	10		
male	35	23	31	8		3
juvenile	30	35	22	2	2	9

During sandbathing the eyes are shut and the ears are laid back against the head. No ventral rub, which is an integral part of the sandbathing sequence in heteromyids (Eisenberg, 1975) was ever performe by _Saccostomus_.

Sandbathing occurred most frequently on sandy substrates; more side-rubs were performed and it was not restricted to specific loci. Sandbathing on soil substrates was less frequent, and normally restricted to specific loci. It is therefore probable that when sand was utilised, the grooming function of sandbathing was predominant, whereas sandbathing in soil had a more communicatory value.

In the latter case, when an animal approached a sandbathing locus, one or more of the following actions would occur: sniffing and/or nibbling at the ground, digging, followed by sandbathing. It can be concluded that a sandbathing locus influences the behaviour of conspecifics, and that sandbathing, at least with soil as a substrate, is usually concentrated at specific points, which however appear to be chosen at random.

Sandbathing in the same loci by conspecifics also ensures that they all bear the same body smell, which is in turn deposited, transferred and picked up from the soil.

It can be deduced from the above data that sandbathing, as well as grooming the individual, plays a significant role in intraspecific chemical communication. Sandbathing is distinctly employed in marking by _Jaculus_ and _Dipodomys_ (Eisenberg, 1975; Laine and Griswold, 1976)

Eisenberg (1967) states that sandbathing is a normal part of the behavioural repertoire in most rodents adapted to arid environments. It is, however, not confined to desert rodents, but the frequency of occurrence and stimuli necessary to elicit sandbathing is characteristi of desert adapted species. In the above rodents it is concentrated at a specific locus and serves as a focus of activity for two or more interacting individuals; this indicates its importance in olfactory communication and marking.

Sandbathing has a further function of dressing the pelage. In desert forms this is important, as many have an increased sebaceous gland skin secretion (Eisenberg, 1963), which serves to reduce water loss through evaporation.

During sandbathing, the whole of the body surface is dusted. If Saccostomus is not supplied with sand, the fur loses its sleek and shiny look, for reasons described above. This occurs in many rodents that sandbathe, emphasising the role sandbathing plays in grooming.

DIGGING AND BURROWING

To observe burrowing in captive Saccostomus, an aquarium was filled to a depth of 20 cm with soil which was watered occasionally and allowed to settle for six months, to ensure compactness. One adult litter, four males and one female,w as placed in one aquarium, and in another a female with four juveniles.

Digging

Digging consists of the following two components (adapted from Eibl-Eibesfeldt, 1951):

Scraping, a simultaneous scratching with both forepaws against the substrate, serves to loosen the soil, which is then accumulated under the body. During foraging, Saccostomus frequently utilise the forefeet to move aside the substrate and this is termed scratching; both or one forepaw may be used. Scratching is not accompanied by a kick-back, as is scraping.

Kick-back. Once sufficient soil has accumulated underneath the body, it is ejected by stretching the hind legs in front of the heap and kicking backwards, always with both hind legs simultaneously. Kick-back is not dependent on the amount of earth accumulated, but is rather a stereotyped movement.

Digging consists of between two to four scrapes, followed by two kicks. A similar method of digging occurs in Parotomys (Nel and Rautenbach, 1974).

Burrowing

Digging of a burrow usually started in a corner, against the side, or against some solid object The soil is initially loosened by digging repeatedly in the same place and the incisors are also used. Initially, digging was not concentrated at any specific locality, but occurred in a random fashion at various sites, till eventually a burrowing site was selected.

All the individuals took turns at digging, and when one moved away, another was always present to take its place; on occasion a few were present in the burrow simultaneously.

Digging frequently started several centimetres in front of the burrow opening, and then proceeded along the length of the burrow. This served to rid the burrow of accumulated soil. This type of digging was frequently performed on the surface; the animal started digging at a given spot and proceeded in a line along the surface, then came back to the starting point to start again. This "surface" digging was more common in females. This surface digging may be an artifact of captivity, where soil for tunnelling is absent. The animals which had burrows were not seen surface digging in this manner. It has also been suggested that digging may be motivated by a desire to escape (King, 1968).

Another way of removing accumulated lumps and pebbles was to carry them in the mouth and/or pouches. All the lumps are removed from the burrow and deposited around its opening, so that the area of the tunnel opening is usually characterised by the presence of lumps (Fig. 21). This behaviour appears to be inherent in Saccostomus. In the holding cages sand lumps, corncob bits and occasionally rat cubes and faecal pellets, as well as nesting material were frequently deposited between the bars and/or on the ledge of the cage (Fig. 22). Ewer (1967) observed the same behaviour in Cricetomys, and suggests this was synonomous with plugging the burrow.' This appears to be the case in Saccostomus, which frequently 'unplugged the bars' during the night.

Saccostomus, like many other rodents, plug the entrance to the tunnel. This is accomplished by pushing at the lumps with the snout, and a

b

Fig. 21 Burrowing in S. campestris

a) tunnel entrance characterised by earth lumps (note animal has pouches filled) and

b) earth lumps on cage edge.

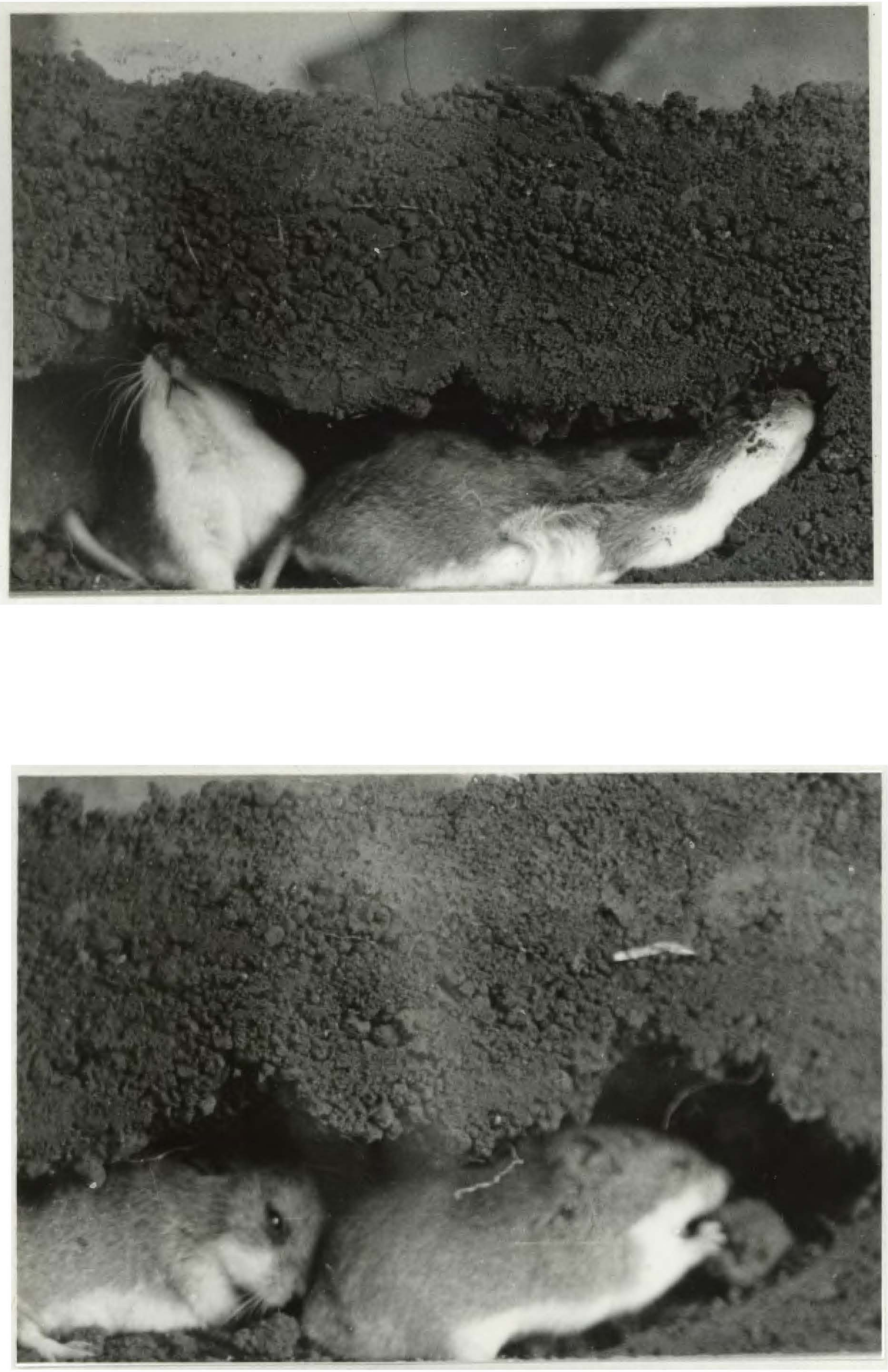

Fig. 22 Burrowing in *S. campestris*.

occasionally the forepaws, which serves both to push them to the entrance, and further to compact them. Eisenberg (1975) suggests that plugging the burrow has the dual function of preventing entrance by predators, as well as helping to maintain a constant humidity within the burrow. The latter is of special importance in rodents living in arid and semi-arid environments, as it helps to reduce water loss through evaporation by keeping a high humidity within the burrow system. Larger obstacles and cave-ins were nibbled at till their reduced size permitted their removal. Obstacles in the roof were removed by turning almost onto the back, and biting at them.

Pushing out earth with the forepaws, as commonly occurs in rats and hamsters (Eibl-Eibesfelt, 1951) was infrequent; the snout was used more often.

During burrowing, the eyes are occasionally closed, especially when digging or turning around in a confined space (Fig. 22). The ears are laid back against the head. Body shaking occasionally occurred after digging in the burrow, but was never seen on other occasions.

Other movements associated with burrowing include <u>levering</u> (Eibl-Eibesfelt, 1951) which consists of a lifting movement with the snout, whereby the earth is pushed up or loosened. Apart from occasional pushing with the snout, no specific packing of the wall was seen, as occurs in heteromyids (Eisenberg, 1963, 1967). <u>Saccostomus</u> is well adapted to digging, having exceptionally strong forefeet. Within the space of two hours a female with four juveniles dug a main chamber and three exit tunnels.

The females appear to spend more time tunnelling and digging. In one situation two males slept and looked after a young litter, while two females tunnelled. It is possible that the female has a more extensive and complex burrow system, as was found in both Gerbillus and Cricetus (Kirchshoffer, 1958); both species are solitary types.

The entrance to the burrow was always sloped, and levelled off after a few inches. Walker (1964) notes that Saccostomus have a separate entrance and exit in the burrow system. In the one aquarium four tunnels leading to the surface were present. Parotomys also have several entrances (De Graaf and Nel, 1965) as opposed to Beamys (Morris, B. 1962) which has a communal entrance and exit.

It is not surprising that digging, which is an integral part of the behavioural repertoire, should also occur as a displacement activity. In this context it was also performed more frequently by the females, and was seldom observed in males.

Saccostomus proved to be very susceptible to cold, and therefore living in burrows could be of great importance in helping maintain body temperature. This applies especially to Saccostomus inhabiting the semi-arid regions, which are subject to extreme ranges of ambient temperatur Rodents living in arid and semi-arid environments escape high ambient temperatures and large daily fluctuations by living in burrows (Nel and Rautenbach, 1974), and further by being nocturnal. It is a significant fact that most of the rodents adapted to living in arid and semi-arid environments are burrow dwellers, plug their burrows, and are also nocturnal.

Variation in digging activity between Saccostomus individuals may be, at least partly, attributed to the fact that they occupy such a wide variety of habitats. As stated in King (1978) the propensity to dig is related to the habitat occupied by the species.

NEST BUILDING

METHOD

Various types of nesting material were provided to test the tendency to build nests and nest building ability through the construction and type of nest built, and preferance for a specific type of nest material. Materials provided were:

(i) Newspaper strips (300 mm x 10 mm). 20 Identical strips were placed halfway into the cage. (This method was adapted from Wolfe, 1970). The number pulled into the cage, utilised for nest construction and the number shredded were determined. The degree of shredding was measured as follows:

A: 20 - 30 cm long
B: 14 - 19 cm long
C: 6 - 13 cm long
D: 0 - 5 cm long.

(ii) 10 g of fine woodwool, deposited in the centre of each cage.
(iii) 20 pieces of polystyrene, deposited in the centre of the cage
(iv) cotton wool or grass, added at random.

The bedding of each cage always consisted of equal amounts of sand and crushed corncobs.

Nests were classified as follows:

1. Closed nest, roofed over and hollow inside.

2. Covered nest (approximately 25 - 50 per cent covering).
3. Rounded nest, with sides and a few strands over the top.
4. Depression, nest material gathered.
5. No nest built and no nest material gathered.

The quality of construction was graded as follows:

+ : material tightly interwoven to form a compact, neat nest.
A : Average
- : material lightly interwoven, and/or scattered around nest.

The physiological state of the animal (pregnant or lactating) as also the sex, were noted. Degree of shredding was also observed. Only adult animals were tested.

RESULTS AND DISCUSSION

Nest building utilising newspaper strips, woodwool and polystyrene is shown in Tables 5, 6&7. All the material, irrespective of type, was usually utilised and some type of nest was made. The best nests were constructed with woodwool. Shredding of the nest material always occurred especially when polystyrene pieces were utilised, probably in an attempt to make the pieces 'fit' better.

Nest building involves 3 basic components:

<u>Collecting</u> Method of collecting depends on the type of nest material provided. Usually all the nest material which is used in nest building is collected prior to the start of construction. Once sufficient material is present, the collection of new material is not so complete, and it may only be partially utilised.

Table 5 Nest building in <u>Saccostomus</u> utilising identical paper strips (figures are percentages).

		Animals		
		males (20)	females (25)	pairs (10)
Amount of material utilised		100	99,8	99
Nest grade	1	25	20	0
	2	35	20	0
	3	35	52	10
	4	5	8	90
	5	0	0	0
Construction:	positive	20	32	30
	average	40	60	60
	negative	40	8	10
Shredding	A	17	17	19
	B	26	36	16
	C	40	30	43
	D	17	17	22
	total	12	5,5	20
Whole strips		88	94,5	80
No. pouched		5,5	10,2	10
No. chewed		7,5	3	8,5

Table 6 Nest building in <u>Saccostomus</u> utilising 10 g woodwool samples (figures are percentages).

		Animals			
		males (24)	females (19)	pairs (13)	male groups (10)
Materials utilised		100	100	98	100
Nest grade	1	20,8	21,1	0	10
	2	25	31,6	15,4	20
	3	29,2	26,3	53,8	30
	4	25	21	30,8	40
	5	0	0	0	0
Construction:	pos.	42	68	54	60
	aver.	50	27	38	30
	neg.	8	5	8	10
Total shredded		16,7	2	7,7	-
Nest bottom covered		54,2	52,6	15,4	10

Table 7 Nest building in <u>Saccostomus</u> utilising 20 polystyrene pieces (figures are percentages)

		Animals		
		males (9)	females (5)	pairs (7)
Materials utilised		100	100	100
Nest grade	1	0	0	0
	2	0	0	0
	3	33	60	71
	4	67	40	29
	5	0	0	0
Construction:	pos.	11	20	28
	aver.	89	80	72
	neg.	0	0	0
Total shredded		22,2	40	28,6
Nest bottom covered		44,4	20	0

Transportation Nest material is either transported in the pouches, in the mouth, or, if bulky, dragged along the ground. Alternatively, the nest may be built on the spot where the nest material is found, especially when woodwool is provided, as, being interwined, it is more difficult to transport. When additional nest material is provided, it is usually transported to the existing nesting area.

Nest building After the nest material has been collected, building of the nest proceeds. *Saccostomus* usually start at the central area of the nest; from this position the surrounding nest material is pulled in to form an approximate ring around the individual. This is accomplished by stretching the body and 'raking' in the surrounding material with the forepaws. The mouth is also frequently used to gather in odd bits. Both the above actions serve to compact the nest material and prevent it from becoming scattered. (Fig. 23).

When the nest material was interwined or bulky, e.g. woodwool, the nest was frequently constructed as follows: the animal would make its way into the approximate centre of the material, from where it would commence to hollow out the area, by a 'hollowing' action (Eibl-Eibesfeldt, 1951). The animal repeatedly walked in a circle thus flattening the nesting material. This movement is accompanied by levering with the snout (the snout is placed under or against the material and pushed) and pulling and pushing with the forepaws to further enlarge the area. Sometimes digging and scratching was performed within the hollow, presumably to remove any material covering the ground surface. Hollowing movements were frequently observed prior to the individual settling down to sleep, in which case it probably served to get the animal more comfortably settled.

Fig. 2.3 Nest building in S. campestris

a) nest construction and b) completed nest.

All types of nests were built, from a shallow depression to a complete covered nest. The latter usually had both an entrance and exit, as also noted for *Peromyscus* (Eisenberg, 1962). Specific individuals tended to build the same type of nest repeatedly, i.e. some were poor builders, some average and others repeatedly built complete nests. This could result from some animals being generally more active, and thus spending more time on nest building. King, Maas and Weismann (1964) noted that more active mice built larger nests.

When within the nest, especially at low ambient temperatures, *Saccostomus* would cover the entrance. This was also observed in *Beamys major* (Hanney and Morris, 1962).

The quality of nest construction is dependent on the following factors:
The amount of nest material provided: If this was insufficient, individuals tended to build a hollow nest with little or no covering.
Type of nest material: with polystyrene pieces construction was inefficient (compare nest grades, Tables 5, 6 and 7) due to inability o the individual to combine the pieces, which were not suitable for nestin
The ambient temperature: It appears that with colder temperatures, the nest was more compactly constructed, with more covering on top (Table 8). However, covered nests were also constructed during summer. Lisk, Pretlow and Friedman (1969) found no correlation between nest size and temperature in *Mus musculus*. However, it appears that adequat nests are important for the survival of solitary *Saccostomus* during colder temperatures. Kinder (1927) and Stiemie and Nel (1973) also stress the thermoregulatory function of nests.
The number of animals present in a nest: The more animals in a nest, the more open the nest was. This also applied to lactating females.

Table 8. Nest building (percent) in <u>Saccostomus</u> during the winter months (M-male, F-female, G-group).

	May			June			July			Aug			Sept		
	M 34	F 27	G 7	M 12	F 11	G 31	M 17	F 12	G 11	M 20	F 15	G 12	M 21	F 16	G -
Amount of Materials utilised	100 percent in all months														
Nest grade 1	18	33	0	67	27	0	35	33	9	25	33	0	15	19	-
2	32	22	0	8	27	26	24	17	9	40	13	17	24	31	-
3	38	19	0	17	27	32	29	33	18	15	33	33	19	25	-
4	12	26	100	8	19	42	12	17	64	20	21	50	42	25	-
5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-
Sites with shredded nest material	81	76	-	92	-	-	88	100	-	60	67	50	38	25	-
Nest bottom covered	47	41	29	75	55	13	88	92	55	80	73	33	43	44	-

Initially, the nest may be totally covered, but as the litter grew older and larger, the nest became open. The lack of an adequate nest in this situation is compensated for by the heat conserved through huddling.

Pregnancy, lactation or the oestrus cycle does not appear to influence the degree and quality of nest construction. Lisk et al. (1969) also found no correlation between nest size and oestrus cycle. Both sexes o Saccostomus are capable of building equally good nests. Wolfe (1970) stated nest building in Peromyscus was also unaffected by sex, whereas Stiemie and Nel (1973) did observe a general tendency for better construction among females.

Shredding, or chopping (Eisenberg, 1967) of nest material occurred frequently, although it differed in intensity between individuals. The material covering the nest bottom was normally the most shredded. It seems probable that most of the material is shredded within the nest although some may also be shredded during pouching. Shredding of nest material is also exhibited by Desmodillus (Keogh, 1973). Layne (1969) notes that scattering and shredding of nest materials is the result of nervousness or displacement activity. This was not the case in Saccostomus. Scattering of nest material was only observed in cages where fighting occurred, and then rarely.

The majority (over 76 percent) of nests were situated in the corners (Table 9); preference was then given to the sides of the cage and finally the central area (less than 8 percent). Kinder (1927) noted that rats tend to position their nests where there is minimal air circulation, i.e. in the corners. This finding is further supported

Table 9 Nest positions (percent) in <u>Saccostomus</u>

	Animals		
	males (175)	females (146)	pairs (13)
Corners of cage	81,7	83,6	76,9
Sides of cage	9,7	10,3	15,4
Central part of cage	5,1	3,4	7,7

by Stiemie and Nel (1973) and the present observations. In Saccostomus over 70 percent of the nests were placed under the food and water trough, at the front of the cage (Fig. 17). This trough is only a few inches above the bedding and the lowest part in the cage. Elimination sites, even more so than nests, are placed in the corners and against the sides of the cage. They were never found centrally situated (Fig. 17).

Hanney and Morris (1962) observed that Beamys regularly removed waste from its nest. This behaviour was not observed in Saccostomus and the nesting areas were frequently full of sunflower seed husks. However, the nest was usually clean as they had specific elimination sites outside the nest. In a few cases faecal pellets were present within the nest; they were always found under the nest material with the larder of food. It is possible that faecal pellets are placed in the larder for purposes of coprophagy, but this appears unlikely due to the scarcity of the practice.

Food was usually stored within the nest area (see Hoarding). However, in 2 percent of males and 3,1 percent of females food cubes were found stored in the elimination site.

Nesting ability appears to be inherent, although it is probably improved with experience. Soon after leaving the nest (at approximately 3 - 4 weeks of age) young were observed carrying odd bits of nest material back to the nest. A six week old male (isolated) was able to construct a fully covered nest, and stock it with a larder, in the adult manner.

Dieterlen (1963) has suggested that nesting is a characteristic of altricial species. In Saccostomus nesting probably has the important dual function of keeping the young warm, and offering increased protection, by restricting movement of very young animals away from the nest.

Chapter 5. SOCIAL BEHAVIOUR

Social behaviour comprises any behaviour patterns involving two or more interacting individuals (Eisenberg, 1962).

COMMUNICATION

Communication makes use of the following senses: visual, auditory, tactile and olfactory.

Visual Saccostomus have large eyes, characteristic of nocturnal mammals. However, sight may not be exceptionally sharp as they do not react to sudden movements. It is probable that their distinct colouring, i.e. white ventrum, and contrasting dorsal surface, is a visual aid in social encounters (see Aggression).

Auditory Several types of sounds are uttered by Saccostomus: a 'twittering' sound in newborn young, from a few minutes post-partum, which later turns into a 'chirping' sound. It is heard almost constantly, and is possibly a comfort sound. It ceases at about two weeks of age. Squeaking sounds are uttered by young in the nest, probably when hungry, and also when picked up or isolated. Sometimes squeaking induced retrieval by the female.

Chattering is caused by grinding the upper and lower incisors against each other. It occurs frequently during threat, in both opponents; the 'chits' increase in intensity as the level of aggression increases. A high pitched squeal is uttered by a frightened subordinate during attack and when pursued. It usually serves to inhibit or delay attack by the dominant.

During sleep, short squeals and grunts are frequently uttered. These may be accompanied by twitching and jerking of the extremeties or sometimes of the whole body, as if the animal is dreaming. *Cricetomys* have also been heard to squeak during sleep (Ewer, 1967).

Tactile stimuli are received primarily by means of the vibrassae. The fur of *Saccostomus* is of varying lengths, and it is possible that the longer hairs may also receive tactile information. Both of these means appear important to a tunnel dweller, enabling it to distinguish obstacles or foreign matter in the tunnel as it moves along. The importance of this means of receiving information has not been analysed

Allogrooming, although infrequent, probably serves to communicate a sense of amicability between conspecifics.

The olfactory sense in *Saccostomus* appears to be well developed, and is probably the most important means of communication. Recognition of conspecifics is usually naso-nasal, as observed in encounters during foraging. When juveniles or conspecifics return to the nest, they are usually investigated by the residents. Recognition of any new individuals is immediate.

Olfactory stimuli are also essential for communicating the state of the female's physiological condition, as shown by frequent naso-anal investigation of the female by the male.

The possible functions of the chemical secretions (discussed under marking) in *Saccostomus* are as follows:

To signify the presence of conspecifics (individual recognition) at the same time serving to space individuals (territory maintenance) and delineating home territory. This is important in a solitary species as information may be conveyed without coming into unnecessary contact with conspecifics.

Reassurance, to increase self confidence during aggression and mating, and to reassure the animal in its own environment.

Marking of the larder.

Appeasement of aggressor, and to indicate submissiveness, but only in cases of extreme aggression.

Promotion of a group smell.

Threat. Ewer (1968) noted that reassurance is usually complemented by intimidation or threat.

MARKING AND TERRITORIAL BEHAVIOUR

Territories may be maintained by physical means, but marking also plays a major role.

<u>Ways of marking</u>

Various means of depositing chemical signs are present in <u>Saccostomus</u>.

<u>Sandbathing and flank glands</u> Sandbathing is the most frequent method of marking (see sandbathing). Ewer (1968) notes that glands occur on the sides or flanks of a number of small rodents that inhabit burrows; the side of the body rubs against the burrow wall during movement, thus rubbing a secretion onto the burrow wall. It is uncertain whether <u>Saccostomus</u> has such a gland (see Study on possible skin glands), where? but the presence of ventral glands would be clearly advantageous for depositing chemical signals in animals that sandbathe.

The possibility of the presence of a flank gland is further supported b the following behaviour: on occasion, especially after an aggressive encounter with a female, a male was seen to rub his side against a branch, the soil or other prominent objects. When rubbing against the soil, the animal would commence by lowering the side of the head against the substrate, followed by a lowering of the body, and a simultaneous push forward, so that the whole side of the body would be dragged against the surface. (The cheek and flank glands rubbed simultaneously in one marking movement). Rubbing of flank glands has also been observed in the hamster (Eibl-Eibesfelt, 1951). The importance of sandbathing in marking, seen in the frequency of occurrence of this behaviour, is obvious when the animal is put into a clean cage; Saccostomus would usually start sandbathing within a few seconds. Marking behaviour has been observed in a few species on introduction into a new environment (Martin, in Johnson, 1973). This behaviour apparently serves to make the area familiar.

Sandbathing, together with huddling, is also of further importance in ensuring a group smell within a family group.

Marking by means of cheek rubbing Rubbing of the cheek area was the second most common marking behaviour observed in Saccostomus. Contrary to sandbathing, cheek rubbing was exhibited primarily by the males. Usually the whole of the side of the head, from the snout almost to the ears, was rubbed; this occurred in a posterior direction, starting at the snout. During the procedure the animal stood on all fours; Cricetomys cheek rubs when standing on their hind legs (Ewer, 1967).

Cheek rubbing occurred during daily explorations, after an aggressive encounter with a female, and during or after mating. Usually only prominent objects were rubbed, i.e. a lump of earth, branch, nesting box and rarely, a female. Cheek rubbing also occurred in conjunction with ventral gland rubbing, as mentioned above.

Snout rubbing has been observed in squirrels (Eibl-Eibesfelt, 1951, and Straschil, 1975) and cheek rubbing in Thryonomys (Ewer, 1968) and male Cricetomys (Ewer 1967, 1968). The latter frequently cheek rubbed during courtship. Quay (1962, 1965) noted the presence of glands at the corner of the mouth in many rodents.

Ventral surface Rubbing of the ventral surface, commonly known as the perineal or anal rub, also occur. The posture is similar to that of stretching: the animal flattens its ventral surface against the substrate by dearching the back, and then pushes itself forward with the hindlegs, so that the ventral/perineal region rubs against the ground. This behaviour was only infrequently observed in Saccostomus.

Lee and Estepp (1971), and Theissen, Blum and Lindzey (1968) describe a mid-ventral sebaceous gland in M. unguiculatus. As Saccostomus rubbed the whole of the ventral surface, it is not clear which part of the ventrum was used for marking. This behaviour was observed a few times, after mating and during normal activity. Johnson (1973) suggests that the perineal rub and cheek marking, as observed in the sexually stimulated male, may serve as a sex attractant and also have a psychological effect by increasing the animal's self-confidence.

The postures assumed during the perineal drag/ventral contact and stretching are similar to each other. Eisenberg (1962) notes that the flexion and extension which occurs in the ventral rub in heteromyids originated from stretching and perineal drag.

Marking by urine and faecal pellets As has been mentioned above (see Elimination) it does not appear that urinating and defaecating sites play any specific role in marking.

Possible urine marking was observed in the following situations: During excessively aggressive encounters, a strong, musky scent, also found in hamsters under similar conditions, was secreted. On occasion this smell was accompanied by a trickle of urine. Unfortunately, the individual responsible could not be determined as they all moved very quickly, but it could have two possible functions:

a) if secreted by dominant animal, could serve as a threatening gesture, or

b) if secreted by the subordinate it serves as a form of appeasement, or defense, as is well known in the skunk.

It seems probable that it was secreted by a subordinate, as it only occurred when one of the two individuals was submissive. In many other situations with two equally aggressive animals, it never happened.

Koenig (in Ewer, 1968) describes the production of a strong smelling secretion in the marmot, Marmota marmota, which he believes has a defensive function. Ewer (1968) also observed urine trails left behind by Cricetomys when they were frightened or anxious. It is suggested that in Saccostomus this strong smelling substance is secreted together with a few drops of urine.

Another instance of possible marking was when a female with nursing young was given a banana peel which she took to the urinating corner, and then proceeded to push it with her snout a few times before turning around and urinating on it in the normal manner. The same female was also observed scratching and pushing with her nose in the food pile, then urinating on it. This particular behaviour was never observed in any other individuals, although in quite a few cases rat cubes were found together with the faecal pellets, separate from the usual larder. The above behaviour could possibly serve to mark an individual larder.

<u>Marking of the larder</u> This is unproved, but it is possible that the gland in the pouch (as described under Pouching, in Ingestion) is a sebaceous secretory gland, the secretion of which would be spread over the rat cubes or seeds, thus serving to mark and identify an individual's larder.

Unfortunately, due to the scarcity of marking behaviour, insufficient data is available to determine the exact effects of marking. Johnson (1973) suggests that the absence of marking may be an artifact of captivity, and that it is probably more frequent in a natural environment. This is probably true of <u>Saccostomus</u>, which is basically a solitary species. Animals placed in a more natural environment, (i.e. a larger cage with earth, branches and nest areas, as opposed to the usual holding cages) showed increased marking behaviour.

SEXUAL BEHAVIOUR

METHOD

Behaviour during mating and sexual encounters was categorized as follows: (adapted from Dewsbury, 1970)

Male behaviour: (i) Pursuit of the female; this usually ended with mounting.

(ii) Mount or attempted mount; a mount was considere successful if accompanied by pelvic thrusts.

Female behaviour: (i) Running - female run from male pursuit.

(ii) Lordosis - mating posture accompanied by concave arching of the back.

Mutual behaviour: (i) Locomotor exploratory behaviour which is not orientated towards partner.

(ii) Genital grooming.

(iii) Grooming other than genitals, including scratching.

(iv) Contact, which consists of naso-nasal, naso-anal and general body investigation.

(v) Motionless - standing still, including while being examined by partner, or in the case of the female, after mating.

(vi) Aggressive behaviour.

(vii) Other unrelated behaviour, i.e. sleeping, eating, digging etc.

Female receptivity was graded as follows (adapted in part from McGill, 1962):

High receptivity - No attempt by female to avoid mounts. Immediate lordosis in response to male investigation. 'Invitation' to male.

Good receptivity - Not always immediate lordosis, may attempt to avoid mount.

Average receptivity - Occasional threat display or rearing onto hind feet when approached by male.

Poor or unreceptive - Immediate threat or attack when approached, or active avoidance.

The following times were also calculated for the male:

Mount latency - time from introduction to female until first mount.

Duration of mount - time from beginning of mount till male dismount

Intermount interval - time from end of one mount till beginning of following mount.

Number of mounts.

RESULTS AND DISCUSSION

Courtship

In many mammals courtship ensures that the male is available when the female reaches her peak of receptivity (Ewer, 1968). Courtship behaviour in Saccostomus is limited to the male following the female, with frequent naso-anal sniffing, nuzzling, and attempts to mount. Allo grooming, although now more frequent than during 'daily' behaviour, is still rare. If highly receptive, the female immediately becomes motionles when approached by the male. Alternately, further genital investigatio by the male will induce lordosis. Similarly, a female in a state of high receptivity assumes lordosis (Fig. 24) when stroked along the back

Initially, the female's oestrus state and thus receptivity is communicated by her smell, as evidenced by frequent naso-anal investigation of the particular female by many of her conspecific males. The female may also indulge in naso-anal investigation of the male(s). The receptivity of the female, as in the hamster (Payne and Swanson, 1970) is also communicated by the level of her aggressive intensity towards the male; i.e. the more aggressive the female (and the less receptive), the less likely is the male to persist in following.

A receptive female is also characterised by her posture as she moves along. Frequently she moves with the tail raised and held rigid. This apparently signifies her readiness to mate, as was observed also in Cricetus (Eibl-Eibesfeldt, quoted by Ewer, 1968).

Pseudo-flight is common in the receptive female. She runs from the male, but when she notices she is not being followed, stops, with lifted tail, and waits for him. Eibl-Eibesfeldt quoted by Kirchshoffer, (1958), calls this 'authentic prude behaviour'. However, psuedo-flights were only observed once actual mating behaviour had started.

Occasionally, if the female 'felt' the male was neglecting her, as when he was preoccupied with genital grooming after mating, she would approach him, sniff him and either threaten him or occasionally attempt to mount him. This had the effect of making the male notice her, and

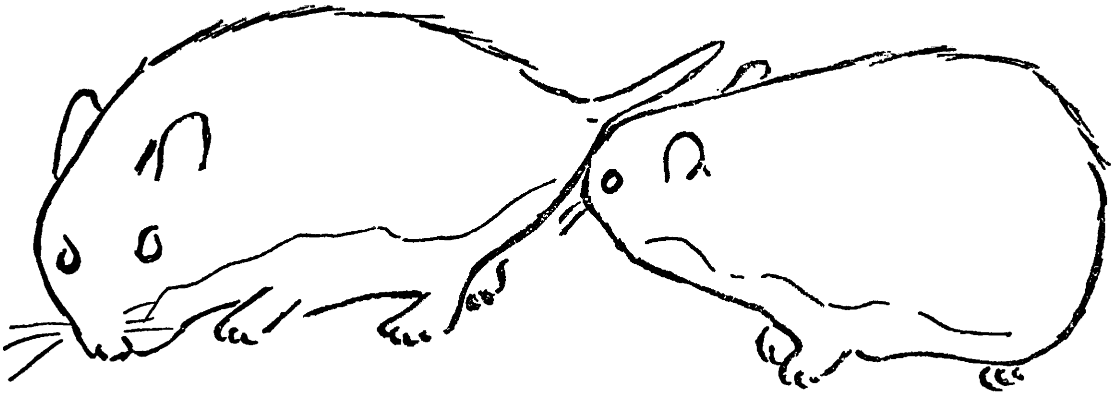

Fig. 24 Naso-anal sexual investigation in <u>S. campestris</u>.

mating usually ensued. This behaviour has been termed as 'incitation to copulate' and has also been observed in Meriones (Eibl-Eibesfeldt, 1951).

Saccostomus never vocalised during sexual interactions, but they may emit ultrasounds. Sales (1972) suggests that ultrasounds could be an important factor in inhibiting female aggression and inducing the female mating posture. Since the female Saccostomus may assume lordosis merely on the approach of the male, it is possible some such form of communication occurs.

If the female is unresponsive, she may rear up on her hindlegs and face the approaching male; the latter usually adapts a submissive posture or crouches; as soon as the female moves on, he follows. However, if the female's aggression increases or persists, the male will usually cease to follow.

Female response is linked with her physiological condition. If she is not at the correct stage of her oestrus cycle, she will be unresponsive, or aggressive. This ensures that the male will waste no time in mating (Ewer, 1968); it also prevents him (to a degree) from sustaining unnecessary injuries.

Behaviour during mating

Mating behaviour is normally displayed in adult male - female encounters. However, it has also been observed in juveniles, where mounting was 'playful' and incomplete, and during aggressive encounters, where the female mating posture was assumed by the subordinate individual.

Mounting of the female is usually preceded by the male sniffing, and occasionally licking her genital area. During copulation, the male clasps the thoracal region of the female with his forepaws; the hind feet are either placed on the females hindquarters, or remain on the ground. No form of grasping of the female's neck, as in heteromyids (Eisenberg, 1963) was observed. Intromission is accompanied by multiple pelvic thrusts, and no lock.

After mating, genital grooming by the male occurs in 80 percent of cases. Grooming may vary in intensity from a few licks to a thorough grooming of the genitals. The latter may also be followed by further body grooming. Genital grooming in the female is less frequent (Table 10) and if it occurs, is not so intensive. After mating the female usually remains motionless for a further mount, or runs off.

Mounting is of short duration, the average being 2,48 s (n = 16). The mean intermounting interval between successive mounts was 10,3 s (range 5 - 7 s, n = 74); this excludes longer intervals during which other activities are performed. Sexual encounters in Saccostomus usually consist of 'bouts' of mating, interspersed with periods of general activity. A typical example is represented in Table 10. In a period of 90 min the male mounted a total of 82 times as follows: 30 successive mounts, 8,48 min unrelated activity, 26 mounts, followed by 10,57 min of unrelated activity; a further 13 mounts with an interval of 3,55 min, followed by a further 13 mounts.

Post-copulatory behaviour

Grooming is the predominant activity characterising sexual encounters

Table 10 Activity during mating (six successive bouts of 10 minutes each) in *Saccostomus*

(n = one pair; M - male, F - female; figures are percentages of total activity during each bout)

Bouts	1		2		3		4		5		6	
Activity / Sex	M	F	M	F	M	F	M	F	M	F	M	F
Locomotor	5,0	12,5	10,0	17,5	27,5	7,5	2,5	12,5	5,0	17,5	-	32,5
Contact	5,0	5,0	5,0	2,5	5,0	-	15,0	-	5,0	-	-	-
Lick genitals	7,5	-	2,5	-	2,5	-	-	-	5,0	-	-	-
Allogroom	-	-	2,5	-	2,5	-	2,5	-	-	-	-	-
Pursuit	12,5	-	5,0	-	2,5	-	5,0	-	-	-	-	-
Run	-	15,0	-	5,0	-	2,5	-	-	-	2,5	-	-
Mount	25,0	-	12,5	-	5,0	-	15,0	-	5,0	-	-	-
Lordosis	-	30,0	-	12,5	-	2,5	-	17,5	-	2,5	-	-
Grooming-body	7,5	22,5	22,5	12,5	12,5	20,0	2,5	30,0	2,5	17,5	-	-
-genital	32,5	10,0	27,5	5,0	7,5	12,5	22,5	-	12,5	-	-	-
Inactive	5,0	5,0	10,0	35,0	20,0	52,5	17,5	37,5	75,0	47,5	100,0	42,5
Other	-	-	2,5	10,0	15,0	2,5	20,0	2,5	-	12,5	-	25,0

(other than behaviour associated with mating). This is especially true of the male, where much of the grooming activity is devoted to genital grooming. The latter ceased almost entirely once mating stopped (Table 11). Grooming by the female is predominantly of the body.

Males occasionally marked (anal rub and cheek rubbing, with the latter predominating) after sexual encounters. Marking is more fully discussed under marking behaviour. The female is usually hyperactive, i.e. increases exploratory behaviour, during and for a short while after mating. Richter (1927) has suggested that the increase in running activity during oestrus is associated with internal drives.

Reproductive potential of the male can be gauged by the position of the testes, whereas breeding activity is reflected by their size. The scrotum of a sexually active male is noticeably enlarged. This change can become obvious within a short period after introduction to a female in oestrus. In Onychomys (Horner and Taylor, 1968) the scrotum also becomes enlarged in sexually active animals. During the non-productive winter months the testes of the majority of the males are abdominal. As summer, and the months during which breeding occur, approach, the testes descend and the scrotums start to enlarge. This is especially noticeable in the paired males. Whether the testes are abdominal or descended appears to depend entirely on the breeding season. Although all the males were non-reproductive during winter, a few males maintained in a colony under a reversed photoperiod and temperatures simulating summer were all sexually active, with noticeably enlarged testes.

Table 11 Activity after peak of mating in <u>Saccostomus</u> (one hour later than table 10; 3 successive bouts of 10 minutes each; figures are percentages of total activity during each bout)

Bout / Activity \ Sex	1		2		3	
	M	F	M	F	M	F
Locomotor	2,5	-	-	5,0	-	10,0
Contact	-	-	10,0	2,5	15,0	2,5
Lick genitals	-	-	-	-	7,5	-
Allogroom	-	-	-	-	5,0	-
Pursuit	-	-	-	-	2,5	-
Run	-	-	-	-	-	2,5
Mount	-	-	-	-	12,5	-
Lordosis	-	-	-	-	-	2,5
Grooming-body	5,0	-	65,0	15,0	2,5	17,5
-genital	-	-	2,5	-	30,0	-
Inactive	42,5	100,0	2,5	77,5	12,5	40,0
Other	50,0	-	30,0	-	-	25,0

AGGRESSIVE BEHAVIOUR

It is commonly believed that intraspecific fighting has the function of spacing individuals (Eibl-Eibesfeldt, 1961). This is important in a basically solitary and asocial species such as Saccostomus.

METHOD

The following tests (adapted from Eisenberg, 1967) were performed to ascertain social interactions:

Encounters in a neutral arena permitted an assessment of the relative amount of aggressive behaviour displayed. By using different type and size cages for the encounter, it was possible to ascertain the effect of space and limited escape possibilities on the encounter.

a) Cage Type A: A standard rat holding cage (370 x 370 x 390 mm) was partioned down the middle with a sliding door in the partition. Two opponents were placed simultaneously in their respective halves of the cage, and allowed five minutes to 'acclimatize'. An exchange of sensory stimuli was possible through the partition, therefore the effect of 'blocked' attack would be observed. Thereafter, the sliding door was opened and subsequent behaviour observed for a further 15 minutes. If aggression was extensive, the opponents were removed to prevent serious injury, as no escape was possible. Actions were recorded by verbal means into a tape recorder.

b) Cage Type B: This cage was the same as the cage used for measuring activity (see Fig. 29, Activity patterns). The central arena was partioned; each opponent had his own nestbox area, a tunnel and the central arena, so that limited escape was possible. The test was carried out in the same manner as in a) above).

Pregnant and lactating females were not subjected to this experiment, for fear of upsetting them.

After each encounter the cages were washed with a mixture of vinegar and water, to remove the scent of the previous occupants.

All the interactions were recorded on a tape recorder, and subsequently analysed.

Behaviours scored were as follows:

1. Introductory acts

Attend - direction of attention towards opponent.
Approach - directed movement towards opponent.
Investigation - only naso-nasal, naso-anal.

Fighting response latency (FRS) - Time (seconds) between permitted entrance (removal of sliding door/partition) and first attack.
The intensity of aggression was determined by the total number of wounds inflicted (bleeding) at the end of a bout.

2. Behaviour during aggression

a) Positive (usually of dominant individual)

Follow - slow movement, maintaining close proximity to opponent.
Chase - rapid pursuit of opponent.
Circling - opponents circling.
Mincing - Small, quick steps.
Threat (offensive) - acts and postures associated with threat.
Attack and fighting.

b) Negative (usually by subordinate individual)

Threat (defensive) - acts and postures associated with threat.

Submission - subordinate lying on back.

Crouch - subordinate remains motionless.

Flee - running away.

3. Mutual behaviour

Investigation - nosing of opponent's body.

Naso-nasal - mutual sniffing.

Naso-anal - investigation of opponent's genital area.

Allogrooming - licking of opponent's body.

4. Other (neutral) behaviour

Exploration - walking around and investigating surroundings.

Selfgrooming.

Displacement activities, in the form of grooming and digging.

Marking.

Sexual activity not recorded, but mounting or assumption of female mating posture out of sexual context were recorded.

Sit or lie - opponent remaining motionless.

Pairing tests Where possible, animals were maintained in pairs (male - female). This permitted an assessment of the male - female relationships throughout pregnancy, parturition and lactation. Female tolerance towards the male was determined, as also the effect of adults, or a previous litter, on the survival of a new litter. A pair and successive litters were allowed to remain together where possible, to establish formation of social groupings.

Group tests   Intersexual groups were maintained to determine social tolerance.

RESULTS AND DISCUSSION

Description of the behavioural components of aggressive behaviour.

The behaviour patterns and postures described below are essentially the same for both sexes unless stated otherwise. The terms dominant and subordinate are used to denote the victor and the vanquished respectively, and refer to the relationship between two opponents.

Introductory phase   Behaviour during this phase is usually mutual investigation, when (social) contact is made, and subsequent relationships determined. It consists of the following components:

Attend - Visual sighting of the opponent causes the individual to either become motionless and watch, or move forward to investigate.

Approach - Approach is usually rapid and results in naso-nasal investigation, threat, attack or flight. The animal being approached turns to face the one approaching.

Investigation - At the initial approach investigation is usually mutual and naso-nasal. The body is elongated to initiate contact, the eyes are wide open and the ears totally or partially erect (Fig. 14); the stretched attention posture.

The response to naso-nasal investigation varies. One animal may flee, in which case it will usually be chased. Alternately, both animals may assume threatening attitudes, or launch into an immediate attack. Occasionally one individual may adopt a submissive posture, or one or both may perform displacement activities. Naso-anal investigation predominates in intersexual encounters and may be performed by both individuals.

Behaviour exhibited during aggression If a social relationship has not been established during the introductory phase, it occurs during this stage.

Positive aggressive behaviour

Threat

The function of threat is to deter the opponent by either driving him away or preventing him from making an attack. Ewer (1968) says threat is a means of discharging aggressive tendencies, which obviates the necessity for fighting. _Saccostomus_ exhibits both defensive threat (intention movement of withdrawal) and offensive threat (derived from intention movement of attack, Ewer, 1968). Threat is usually characterised by an upright posture; the animal stands on its hind legs, and the forepaws are held in front. During the upright posture the white ventrum is exposed as a visual display. Eisenberg (1967) suggests this produces a contrasting reflecting surface which aids in orientatio during mutual uprights. This would be of special value to a nocturnal species, such as _Saccostomus_.

During threat the ears are partially or totally laid back against the head; this appears to be dependent on the intensity of aggression. The eyes are narrowed. In offensive threat the mouth may be opened, revealing the large incisors.

Occasionally, a sideways presentation, which is frequently accompanied by a swaying motion of the body, is given. Sideways threat appears in more intense levels of aggression, and is usually followed by attack, as in e.g., Otomys (Davis, 1972). The swaying of the body is probably a preliminary to lunging at the opponent. Ewer (1968) emphasizes the intimidatory aspect of the stance during threat, as the maximum body surface area is exposed, thus seemingly enlarging the animal

A characteristic form of threat in many pouched species is to inflate the pouches with air, thus making the head look larger (Ewer, 1967, 1968). This behaviour was absent in Saccostomus.

Threat is frequently accompanied by chattering or tooth gnashing when the upper and lower incisors are grated against each other. Chattering, an intention form of biting according to Ewer (1968), is performed during both defensive and offensive threat, but not by submissive animals. Therefore, as in voles (Clarke, 1956) it appears to be performed by dominant individuals or those of equal or almost equal rank.

Chattering was occasionally heard when attempting to handle an individual, especially after a particularly aggressive encounter, when the intensity of aggression was still high. Some animals persisted in chattering after they were separated and the opponent was no longer visible.

Table 12 Behaviour prior to attack in dominant and subordinate individuals of Saccostomus, (Percent of total activity)

Activity	Animal	
	dominant	subordinate
Threat	16,7	37,5
Investigation	20,8	6,3
Chase	20,8	-
Attend	4,2	-
Fighting	8,3	-
Displacement activity	16,7	12,5
Exploration	4,2	-
Motionless/sit	4,2	6,3
Mark	4,2	-
Flee	-	37,5

Chattering as a threatening gesture is common in rodents (Eibl-Eibesfeldt, 1951; Ewer, 1967 and 1968) and is characteristic of those species that attack by biting. In some species it is purely a defensive gesture (Davis, 1972) and in others only exhibited by the dominant individual (Morris, 1962). Ewer (1968) notes that chattering is the usual way of accentuating threat where visual signalling cannot be very effective. In a tunnelling and nocturnal species, such as Saccostomus, this factor is important as intruders may be threatened prior to visual sighting.

Attack

One individual, usually but not always the dominant one, jumps on the other. In the dominant individual attack is usually preceded by investigation or chasing of the opponent. Threat prior to attack by th dominant was infrequent, whereas in the subordinate threat and flight initiated attack most often (Table 12). In many instances the dominant attacked from behind with no warning.

Ewer (1968) notes that although attacks without threat are rare, when they do occur they are never hesitant or half-hearted, but carried out to the fullest extent and with great rapidity. This applies precisely to Saccostomus during highly aggressive encounters. The absence of threat prior to attack by some individuals may be partly attributed to the restricted area, and therefore increased intensity of aggression It may also serve to emphasise the aggressive nature of Saccostomus in a restricted environment.

Attack is most frequently followed by flight of the subordinate, which usually initiated further chasing. Alternatively, in 28 percent of the cases, attack led to further fighting (Table 13).

Fighting

Both individuals grasp each other with all four feet so that their ventral surfaces are pressed together. This 'roll ball' type of fighting in Saccostomus occurs during high intensity aggression, and is usually accompanied by biting; serious injuries may be inflicted.

During roll ball fighting animals are frequently nose to tail (Fig. 25 or with the body at right angles towards each other (Fig.25). As a result bites are most frequently inflicted on the tail, rump area, snout and armpits or lower shoulder areas. In many instances the opponents had to be separated to prevent fatal injuries. Frequently after fighting, the opponents were slightly wet, either from urine or from being mouthed.

Eisenberg (1963) observes that locked fighting is more common in quadrupeds, while sparring predominates in bipeds. Although sparring o grappling as such did not occur, it was common to see both individuals paw at each other in an upright posture. This is called 'rearing up', or boxing, and frequently led to proper fighting, as is characteristic of many rodents (Ewer, 1968). It appears as if both opponents are testing each other. This behaviour is more specifically characteristic of individuals of more or less equal rank, and in milder forms of aggression.

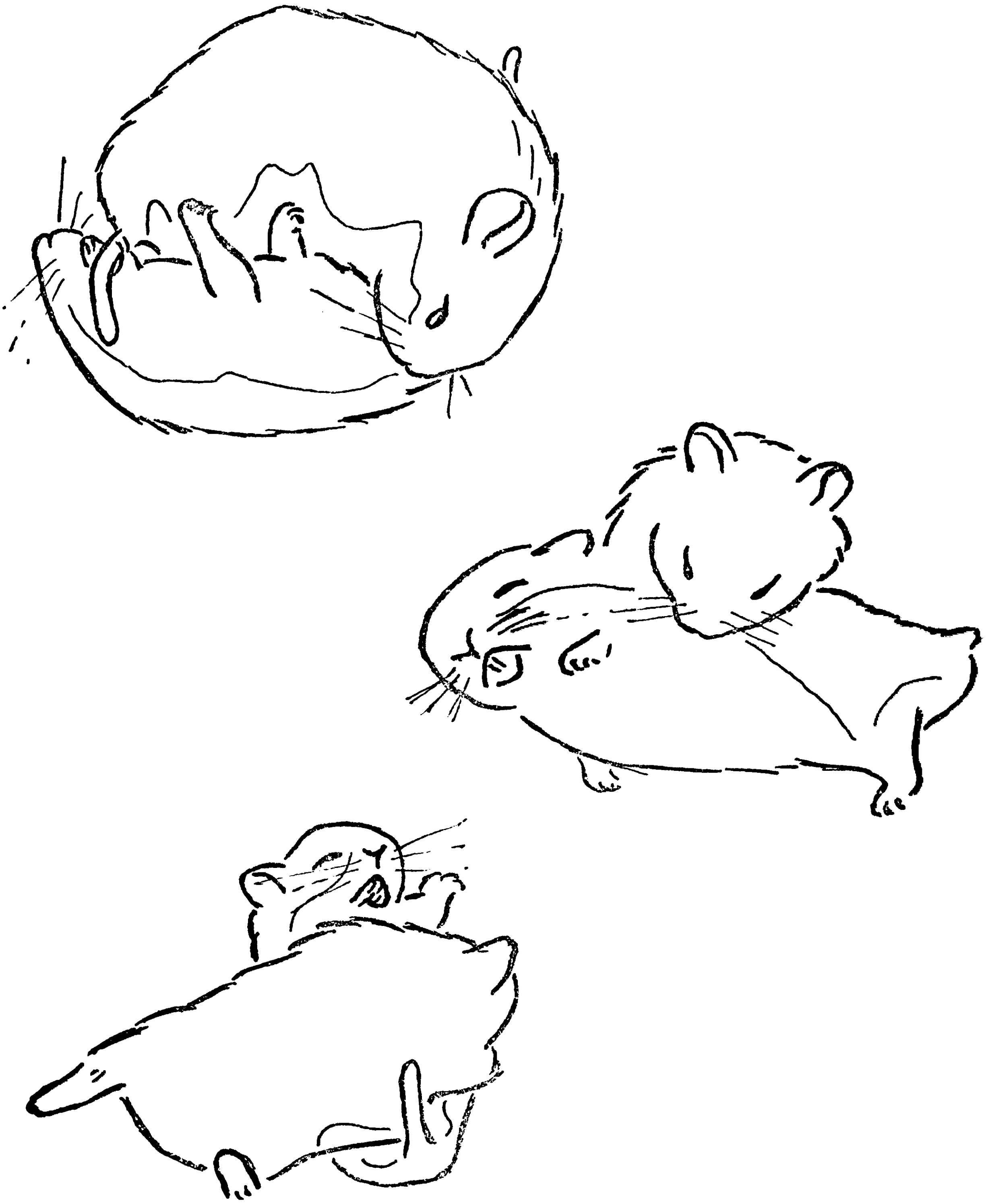

Fig. 25 Fighting in *S. campestris*.

Table 13 Behaviour following attaxk in dominant and subordinate individuals of Saccostomus (Percent of total activity)

	dominant	subordinate
Threat	20	14,3
Investigation	12	-
Chase	32	-
Fighting	28	9,6
Displacement activity	4	-
Submissive behaviour	4	9,5
Motionless/sit	-	9,6
Flee	-	57,1

Circling

Circling was not a consistent part of the aggressive sequence, but occurred, as rearing up, in individuals of equal rank. It may occur prior to attack; both opponents walk around each other, interspersing walking with threat. Circling probably also serves to test the opponent.

Mincing

Short, rapid steps are taken, with the individual in a somewhat humped up posture. This behaviour, which was rarely observed, was interpreted as a combination of aggression and defensive attitudes, as the individual, although clearly subordinate, attacked the dominant individual. It is probable the individual was in a state of conflict.

Escape and 'negative' behaviour

Threat

The most frequent behaviour of a subordinate during an aggressive interaction was threat and fight (Table 14). The subordinate frequently adopts a threatening posture when the dominant approaches. Defensive threat functions to prevent or delay attack in some instances.

Flight

A fleeing opponent usually elicited chasing. In a few instances chasing by the victor was so persistent and accompanied by such

Table 14 Activities (percent) of <u>Saccostomus</u> during 15 min encounters in a closed arena (male n = 3, female n = 2; dom - dominant, sub - subordinate)

Behaviour	Males		Females	
	dom	sub	dom	sub
Introductory	0,8		0,7	4,8
attend	0,8		0,7	3,2
approach				1,6
Aggressive	46,4	56,9	16,9	18,7
threat	13,6	19,2	3,3	7,4
attack	13,6	1,8	6,6	
follow/chase	9,6	0,9	1,7	0,8
flee		18,4		9,7
fight	8,8	13,8	5,3	1,6
submit	0,8	2,8		0,8
Mutual behaviour	32,0	13,8	19,0	11,3
investigate	19,2	3,7	10,5	6,5
naso-nasal	6,4	6,4	5,9	4,0
naso-anal	6,4	3,7	2,6	0,8
Other	20,8	29,3	63,4	65,2
explore	10,4	1,8	27,6	14,5
groom		4,6	15,1	14,5
displace	2,4	14,7	7,3	5,6
sexual behaviour		0,9	0,7	
inactive	1,6	6,4	12,7	29,8
gustatory	6,4	0,9		0,8

aggressive attacks, that the opponents had to be separated. In the larger cages, chasing ceased once the fleeing individual disappeared from sight. However, it would frequently be resumed when he/she was spotted again. This partly supports Moyer's (1968) theory that aggression is stimulus bound.

When very frightened, Saccostomus attempt to bury themselves in the bedding. If insufficient bedding is available they at least try to bury the head. It is possible this 'burying', which serves to cut off all sensory stimuli, may simulate running into a burrow in the wild.

Attack

Attack was initiated by the subordinate on a few occasions. The subordinate would attack, then when the opponent responded, immediately adopt a submissive posture or run away. Originally, this was thought to be caused by nervousness. Seward (1945 a) suggests this behaviour may be due to an unstable equilibrium between aggression and submission However, Moyer's (1968) theory appears more applicable to the present situation. He calls this behaviour fear induced aggression. One of the components of the stimulus situation eliciting fear induced aggression is a degree of confinement in which the defensive animal is cornered and unable to escape.

During chasing bites are frequently inflicted on the rump and tail, and occasionally on the back. In paired animals, the female attacks the male so frequently, that the majority of males are eventually left with out tails or with stumps only. Tailbiting is also common in Peromyscus (Eisenberg, 1963).

Defensive behaviour

In the subordinate, behaviour is mostly confined to defense and escape reactions (Table 14), and watching of the opponent. During low intensity defense the animal remains in the upright posture, with the forepaws extended in front of the body to ward off attack. The eyes ar partially closed and the ears set back (Fig.26). At greater intensity the subordinate lies on his side or back in the full submissive posture (Grant and MacKintosch, 1963) (Fig. 27). The paws are held out to ward off attack, the ears are laid flat against the head and the eyes may be totally closed. This posture, however, did not always prevent further attack

Scott and Fredericson (1951) note that the attitude of defense exhibited by the subordinate becomes more and more stereotyped with repeated defeats, until it assumes the defensive posture in a mechanical way similar to a reflex action. They call this a 'submissio reaction'. This was observed in subordinate Saccostomus, even to the extent that if they were looked at by the dominant, they would immediately flee or crouch. They were not usually pursued.

Squealing

Squealing by the subordinate individual proved to be a highly effective defense mechanism; usually it subdued or inhibited the aggressor and delayed further attack. Squealing was most frequently heard when a individual was threatened, and accompanied the upright defense posture. One subordinate male repeatedly squealed when the dominant merely looked at him. Squealing is limited to subordinates, and appears primarily in males.

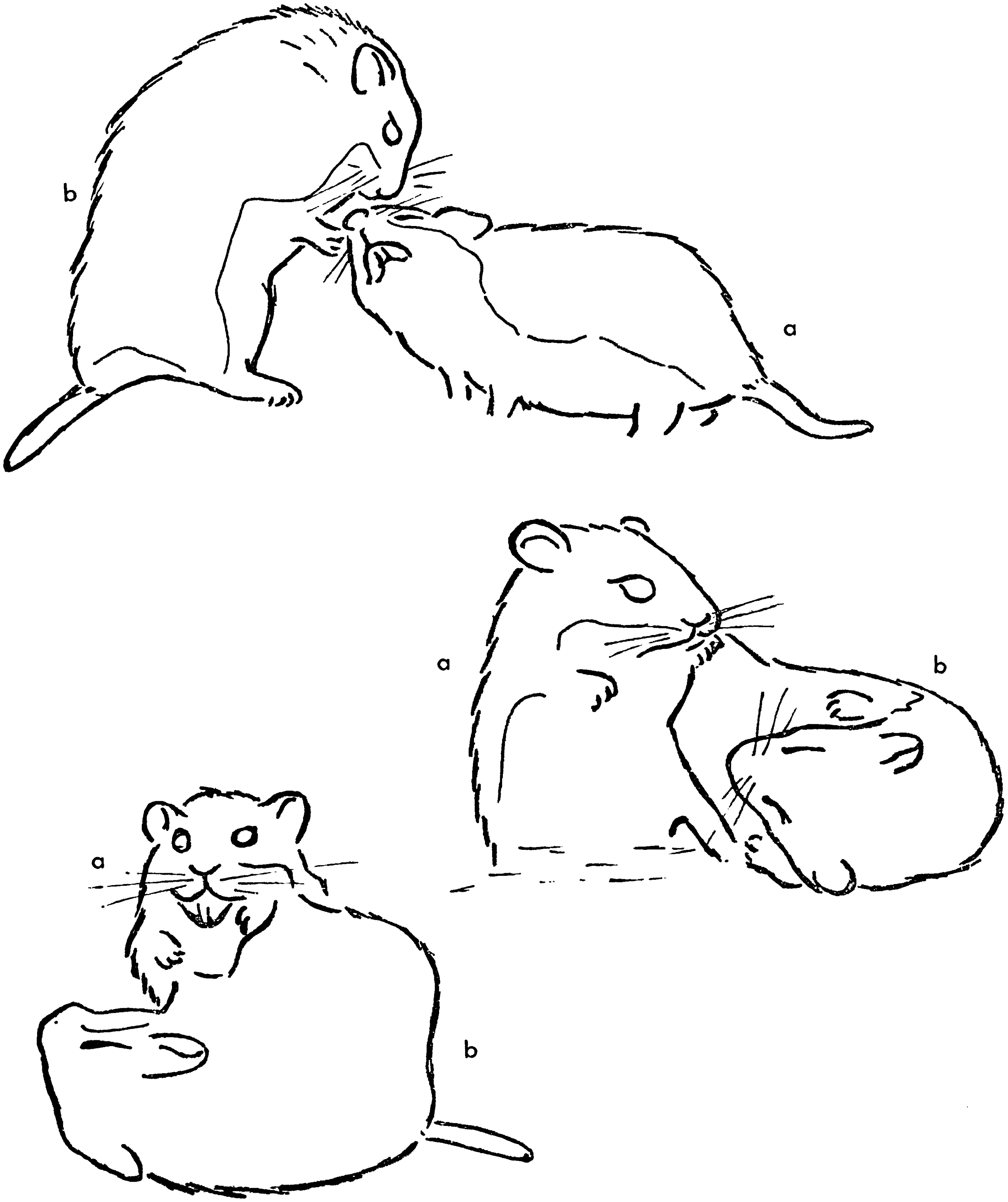

Fig. 26 Postures encountered during aggressive encounters in <u>S. campestris</u>: offensive (a) and defensive (b) threat.

Fig. 27 Postures exhibited during aggressive encounters in *S. campestris*: offensive (a) and defensive (b) threat, and submission (c).

Seward (1945 a) suggests that the freezing, squealing and grooming behaviour of the subordinate serves in a protective capacity, by reducing to a minimum the stimulation for aggression. In captive *Saccostomus* the above factors reduced aggression, but were counterbalanced by lack of space.

A further mechanism limiting aggression is through 'cut-off' postures. Chance (1962) notes that cut-off postures are exhibited by the threatened animal which adopts a posture so as to effectively exclude the aggressive partner from view, at the same time allowing the threatened animal to remain close. A cut-off posture therefore serves to eliminate the releasing elements of a stimulus, i.e. it controls specific arousal during an aggressive encounter.

The most common cut-off posture was to groom, usually with the back turned towards the opponent; e.g., when the dominant approached or threatened, the subordinate immediately sat down and started to groom and appeared to ignore his opponent; this usually effectively inhibite attack. Cut-off is also common in the hamster (Grant, Mackintosh and Lerwill, 1970).

Appeasement and submissive behaviour

Clarke (1956) defines appeasement as that behaviour which prevents consummation of the aggressive drive in the opponent, possibly due to lack of stimuli necessary to release attack. A totally submissive individual lies on its back, with the white ventral surface exposed and, contrary to the supine defensive posture, the paws are limp and the eyes closed (Fig. 27). The ears are also relaxed and therefore not laid flat. According to Chance (1962) the closed eyes serve as a 'cut off'.

Ewer (1968) mentions that appeasement is important in a solitary species to prevent the victor from continuing the attack. However, total submission in Saccostomus did not always prevent further attack. The end result of such persistent attacks was never observed, as the opponents were separated to prevent further injury.

Assumption of the female mating posture was rarely performed by subordinate males, and usually then when chased. This probably served to distract the dominant from his aggressive intentions.

Mutual behaviour

Investigation

An intensive nosing of the opponent's body by both protagonists was sometimes performed between, or prior to, attacks. This type of investigation is not performed by highly aggressive individuals. The areas most frequently investigated were, in order of occurrence, the side/ventral surface, ear, rump, under the chin and back. During nosing one or both forepaws may be placed on the opponent (Fig. 28).

Allogrooming

Allogrooming is one of the main contact-promoting mechanisms in a communal species. Allogrooming was never observed in an aggressive encounter, and very rarely in non-aggressive encounters. In the latte

Fig. 28 Mutual investigation in S. campestris; a) displacement grooming.

case it is brief and consists of a few licks. It is usually performed during intensive nosing of the opponent's fur. Lack of social grooming in Saccostomus can be attributed to the asocial nature of the species.

Other behaviour

Exploration

Exploration was more intensive in the larger cages. This can be attributed to two factors, i.e. larger area to explore and fewer encounters; therefore less time is spent in aggressive interactions. In both sexes, the dominant individual explores the most, and females also tend to explore more than males (Table 14).

Displacement activity (digging and grooming)

Often one, or both, opponents interrupt a threatening display with a bout of grooming activity, which may vary in intensity and duration. Clarke (1956) and Seward (1945 b) suggest displacement grooming serves as an alternative satisfier or tension reducer, resorted to when the aggressive impulse is blocked. In Saccostomus displacement activity appeared to inhibit or delay attack. Subordinate males appear to be more in conflict during an aggressive encounter than subordinate females, as shown by higher level of displacement activity in the former.

Physiological changes accompanying aggression

The following aspects were not consistently observed during each aggressive encounter, so it is assumed they depend, at least partly, on the intensity of the aggressive reaction:

Pilo-erection sometimes occurs during threat, but appears restricted to the thoracal area. The function of pilo-erection is assumed to be intimidatory, as it enlarges the visual size of the individual. In one female the black V mark on the forehead was clearly defined during pilo-erection; this could serve to enhance threat.

Defaecation was resorted to by frightened subordinates. Urination occurred frequently during an encounter, and is further discussed under marking. Ewer (1968) reports that urine dribbling is common in both opponents in encounters of <u>Cricetomys</u>.

In <u>Saccostomus</u>, as in hamsters (Payne and Swanson, 1970) and rats (Barnett, 1963), there appears to be some degree of correlation between the body mass and success during an aggressive encounter. In 70 percent of males and 66 percent of females, the successful (dominant) individual had a greater body mass.

Sensory cues eliciting attack.

Sensory cues eliciting attack are unknown, but probably include olfactory and visual stimuli. In <u>Saccostomus</u> family recognition appears to be primarily olfactory; the smell of a stranger usually precipitates attack, as in mice (Tollman and King, 1956; Ropartz, 1968). Solitary individuals frequently attack an opponent prior to investigation, and appear to react to the mere visual (movement) presence of another individual.

Therefore in animals maintained in a family group, olfactory stimuli appear to be the most important in initiating aggression, whereas in individuals maintained in a solitary state, visual stimuli appear to be equally, or in some cases, more important.

Establishment of Dominant - Subordinate (D-S) relationships

Under stable conditions and in an established family group, the adult female is dominant, as was also observed by Choate (1972). Female dominance is reflected by e.g.,

Higher level of aggression; in intersexual encounters dominant, irrespective of weight of male.

Higher intolerance of conspecifics. All-female sibling groups could not be maintained beyond puberty without serious injury to one or more members, whereas all-male groups frequently were stable.

In paired or family groups, the (dominant) female had little or no injuries; injuries on other members were evidence of continual chasing and biting.

In a group with more than one adult female, breeding in subordinate females was usually inhibited.

The female of *Perognathus pacificus* (Bailey, 1939) and the *Desmodillus* female in oestrus (Keogh, 1973) are also dominant, similar to *Saccostomus*. Female aggression in *Saccostomus* does not appear to be entirely dependent on hormone levels, as is the case in mice where female aggression is associated with lactation (St. John and Corning, 1973). Although a slight increase in aggression usually occurs a few days prio to parturition, the level of aggression is fairly stable in the female individual.

Saccostomus appear to establish the D-S relationship only once within an encounter; this then remains stable thereafter. The D-S relationship may also, although infrequently, appear prior to an encounter, with no fighting, or it may be established at the outset or within the first few minutes of an encounter.

Two basic types of dominant individuals were observed:
An individual that repeatedly attacked a subordinate, despite all the latter's attempts at appeasement or escape.
An individual that ignored, or occasionally threatened the subordinate. The latter situation is partly dependent on the subordinate's behaviour

Development of aggression and factors influencing it

The majority of playful actions in juveniles later lead to actions used in aggression. As the young mature, playful fighting may turn into a real fight if one animal involuntarily inflicts pain on another. Scott and Frederickson (1951) note that paid is the most important factor in producing defensive fighting in mice.

The onset of aggression in Saccostomus also appears to coincide partly with sexual maturity, as also observed by Scott and Frederickson (1951) for mice. However, development of aggression is also dependent on the social status of an individual, and not only its age. Littermates raised together exhibit less aggression than socially isolated individuals. The same was true of mice (Scott and Fredericson, 1951) and hamsters (Kirchshoffer, 1953). Kirchshoffer attributes this to a process of passive inhibition. Aggression tends to increase with the length of the solitary period; Wise (1974) observed a significant increase in female hamster aggression with isolation.

Handling does not appear to affect aggression in Saccostomus. All individuals were frequently handled, and aggression was very rarely shown towards the handler.

It is emphasised that space, or lack of it, is a critical factor in the outcome of aggressive encounters. In a confined space aggression was intensified as a fleeing animal could not escape from the visual field of the dominant, and was usually repeatedly chased and attacked. The above situation is also true of hamsters (Lerwill and Makings, 1971

It is probable therefore that aggression in the wild is not so intense as in captivity, as avenues of escape are always open. Saccostomus is a very docile species, and may even be handled immediately after capture. It seems unlikely that such a tractable species should be so intensely aggressive interspecifically.

Fighting behaviour in Saccostomus differed only so far as intensity of aggression was concerned, so it can be presumed that fighting patterns in Saccostomus are innate and fixed behaviour patterns, as also suggested by Eibl-Eibesfeldt (1961).

ALLOGROOMING

Allogrooming occurs infrequently, probably due to the asocial nature of the species. However, in juveniles allogrooming is more common. This situation is also found in Otomys, another solitary species (Davis, 1972). It can be attributed to the greater social and playful nature of the young; also grooming activity in the young is mostly restricted to the nest. In its confines a young when grooming may accidently lick part of an adjacent littermate, and thereafter continue grooming it. Allogrooming in the nest between adults, which was very rare, may also be at times attributed to the above.

Allogrooming between adults, when it did occur, was most frequent durin sexual encounters. Allogrooming is mostly restricted to the dorsal and neck regions, although any part of the body may be involved.

ACTIVITY DURING CONFLICT SITUATIONS

In conflict situations, Saccostomus have been observed to perform some of the following behaviours:
Intention movements, where the animal 'obeys' all activated drives, and performs a section of each. This was occasionally seen in especially females, when placed in a new environment. The drives of pouching, fleeing and exploration were simultaneously activated. In this situation the animal would frantically pouch food or nesting material, at the same time rushing around and sniffing (exploratory) and also trying to get out of the cage. All the movements were hurried, and although having parts of the normal behavioural repertoire, were incomplete. The situation in which young were pouched (Earl, 1977) was similar to the above.

Displacement activity is an activity which is performed totally out of context with the situation. Bastock, Morris and Moynihan (1953) define displacement activity as "an activity belonging to the executive motor pattern of an instinct other than the instinct(s) activated". There are two situations during which these activities may occur:

Firstly, when two or occasionally more incompatible drives are strongly activated, each drive prevents expression of the other, so that a third act is performed. This third act is a result of the reduction in the inhibitory effects of the drives initially activated (Van Iersel and Bol, 1958). During or after an usually aggressive encounter, one individual may break off activity and proceed to groom, dig or eat, instead of fighting or fleeing. Grooming was the most frequent form of displacement activity and was usually restricted to a rapid face wash. In *Cricetomys* grooming is also the most frequently exhibited form of displacement activity (Ewer, 1967).

Digging as a displacement activity has become highly specialised in both *Dipodomys* (Eisenberg, 1975) and in *Gerbillus*, whereas in *Saccostomus*, only the hind legs are utilised, and it is more common in females.

Displacement activities may be performed by an animal in which one drive is simultaneously thwarted and activated; when a male fell off a branch, he would frequently perform a few face wipes in a bewildered fashion. In this case the urge to flee was simultaneously thwarted, by uncertainty as to 'what to do', but also activated, by flight. The same situation was also observed when juveniles were being weighed and measured.

Displacement activities are derived from activities that are an intrinsic and integral part of the daily behavioural repertoire. This was also noted by Barnett (1956) and Pruitt (1957).

In <u>Saccostomus</u>, displacement activities most frequently occur during aggressive encounters, when they often served to inhibit attacks by the opponent. This tends to support Chance's (1962) suggestion that displacement activities serve the all important function of maintaining a flexible behaviour. It can therefore be concluded, contrary to the observations of Van Iersel and Bol (1958) that the act performed as a displacement activity is not a complete behaviour pattern; further, it is usually irrelevant, and out of context, to the activity being pursued at that time.

<u>An overflow activity</u>, which is "a reaction to suboptimal stimuli" (Bastock et al, 1953), occurs when an animal has one drive strongly activated and the releasing stimuli indispensable for the performance of the executive motor patterns of the drive, are inadequate. The releasing threshold may be greatly lowered, and activity may 'go-off' in response to the most meagre of abnormal stimuli.

The above situation was clearly observed in some subordinate individuals where the flight drive was strongly activated. When the dominant animal even looked in their direction from a distance, the subordinate would instantly turn and flee. This behaviour was only observed in male subordinates, never in females.

Chapter 6 TORPIDITY

Hibernation is characterised by stupor, and by a sharp reduction in the metabolic activity, oxygen consumption, heart rate and respiratory rate. The body temperature decreases until it approximates that of the environment. Hibernation is associated with unfavourable environmental conditions and generally occurs over extended periods (Schmidt - Nielsen 1961). Torpidity is characterised by brief periods of inactivity, where the physiological changes may be as above, but no preparation is necessary.

During winter most of the Saccostomus individuals were kept in an unheated laboratory; nesting material supplied was utilised in all the cages. Many of the individuals exhibited daily periods of inactivity, presumably torpor. During torpor, Saccostomus were totally inactive, not even exhibiting the twitching which commonly occurs during sleep. They were not easily roused and could be picked up and stroked for several minutes prior to awakening, which they did very gradually. Torpor was accompanied by a lowering of the body temperature so that the individual felt cold to the touch. Unfortunately, no internal body temperatures were recorded. Beer (1961) found that Perognathus exhibited torpor at approximately 5°C.; prior to that they were lethargic. No other physical differences, such as body mass increase, were observed in Saccostomus, nor was there any apparent increase in hoarding activity. Bartholomew and Cade (1957) note that in Perognathus, which only hibernates for short intervals, neither fat storage nor food accumulation occurred.

Hudson (in Morton, 1978) notes that many small species of mammal undergo periods of torpor in the laboratory in response to food deprivation and/or cold. Although Morton (1978) found daily torpor in both *Mus musculus* and *Sminthopsis sp*. it only occurred in those individuals not sharing nests (huddling conserves 12 to 30 percent of the total heat energy generated). Similarly, in *Saccostomus*, torpor was only exhibited by solitary animals. Torpor never occurred during warm ambient temperatures and therefore can be attributed to cold, and not to food deprivation, (as the latter was always in plentiful supply). Pitchford and Visser (1970) also note that *Saccostomus* is intolerant of temperature extremes.

It is probable that torpor exhibited in the laboratory is an artifact o captivity, as *Saccostomus* in the wild live in burrows and utilise nests, and are thus protected from the low ambient temperatures.

Chapter 7 ACTIVITY PATTERNS

METHOD

Individuals were tested on two types of apparatus in order to establish the basic activity cycle; data on the frequency of various types of activity were obtained from darkroom observations.

The four-chambered apparatus (Fig. 29) consisted of four separate areas, so that four individuals or groups could be tested simultaneously. Each area consisted of a nestbox joined by a passage to a central area. The latter could be partioned off, so that each group or individual was separate, or it could be left so that the individuals had access to the other nestbox(es). The flooring of the central area consisted of wire, the nestbox and passage of wood, and the whole was covered by perspex, which was removable in the nestbo and central areas. A treadle was situated in the passage and any movement across it was monitored on an Angus Esterline event recorder. Individuals were given a minimum period of two days in which to acclimatise.

The second apparatus used was an activity recorder. This was set at a sensitivity level of 60 percent, so that only definite movements should be recorded, and not just any twitches. In this experiment the normal holding cage of the individual was placed on the activity recording apparatus. No acclimatisation period was necessary as the individual(s) remained in its original cage.

NB	Nest box
T	Treadle
C	Central arena, with movable partition

Scale 1mm = 20mm

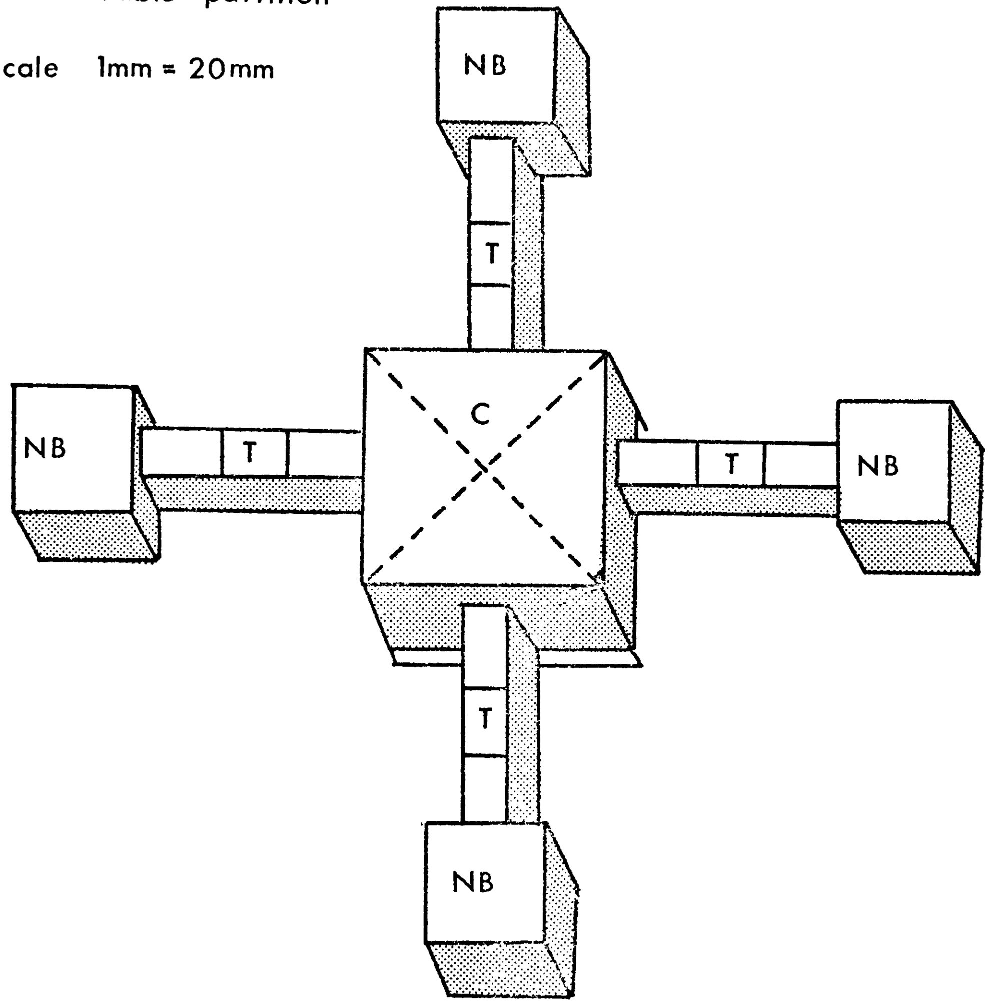

Fig. 29 Four-chambered apparatus for testing activity in *S. campestris*.

Individuals were tested over a period of three months, from June to August. The mean maximum temperature in the room was 20°C and the minimum 17°C. In all, 13 different individuals were tested over an average period of one week each on each type of apparatus. The test animals consisted of six males and seven females; two of each sex were wild bred, while the rest were bred in the laboratory. During the testing periods the individuals were subjected to the minimum disturbance, only being fed and watered if required, but generally the food lasted over the entire test period.

The results obtained from the above experiments were calculated to a percentage base of total activity for each individual, over hourly periods. The mean of these percentages was subjected to one-way, two-way and three-way analyses of variance, using a Wang computer. Each 24 hour period was divided, in order to facilitate the computerisin of data, into a 12 hour day (07h00 - 19h00) and a 12 hour night period (19h00 - 07h00). This also happens to be the approximate day : night ratio during winter. In all the computer analyses the day : night period had to be separated, as otherwise all the other differences which were of significance, would have been obscured.

Observations on mated pairs and family groups were carried out in a darkroom during the dark phase of a reversed photoperiod (10:14 hour cycle, with darkness from 06h00 - 16h00). A red light, which did not affect the animals in any way, permitted viewing. Individuals in the darkroom were housed in two aquaria (32 x 32 x 61,5 cm) and a cage (93 x 88 x 59 cm). The substrate consisted of soil, sand and corncobs; branches and a nestbox were placed in each cage and food and water were supplied ad lib.

The occupants of each cage were observed for a half hour period at 08h00, 10h30 and 13h30, and occasionally at 15h30. Activity was recorded every 15 s (timed by a stop watch), onto a tape recorder. The frequency of each activity was recorded, and not the duration. The total recording time of data analysed was 25,5 for males, 99 for females and 63 for juveniles.

RESULTS AND DISCUSSION

The data resulting from the four chambered apparatus (App. A) are more indicative of exploratory, and to a certain extent foraging, activity, as only those movements were recorded that occurred between the nest box and the central area. On the other hand, the activity meter (App. B) recorded all types of activity, i.e. grooming, eating and other activity occurring within the nest area. (Compare differences in Tables 15 to 20).

There was only a minimal difference occurring in the amount of activity in any one individual between the various days. This shows that the animals were already acclimatised, especially in App. A, as exploratory and foraging levels remained the same. Food pellets, which were made available in the central area, were all normally carried to the nestbox by the end of the first day, therefore any activity associated with this may be ignored.

Data from the one-way analyses of variance (Table 15 and 16) showed a significant difference ($\alpha = 7,94$) in the amount of activity occurring between grouped and solitary individuals. Grouped individuals were more active during the day (41,6 percent of total

Table 15 Difference in activity between grouped and single individuals of *S. campestris* using the activity recorder (D represents day, N night)

Source of variation	Degrees of freedom		Sum of Squares	Mean of Squares	F value
Effect	1	D	27,2001	27,2001	18,3108****
		N	27,9288	27,9288	19,8265****
Error	1	D	32,6803	1,4855	
		N	30,9905	1,4087	
Total					

F (1,22) α = 7,94 (99%)****

Table 16 Difference in activity between grouped and single individuals of <u>S</u>. <u>campestris</u> using the four-chambered apparatus (D represents day, N night)

Source of variation	Degrees of freedom		Sum of Squares	Mean of squares	F value
Effect	1	D	8,3426	8,3426	3,5497**
		N	9,5508	9,5508	2,0185
Error	1	D	51,7048	2,3502	
		N	104,0943	4,7316	
Total					

F (1,22) α = 2,95 (90%)**

Table 17 Differences in activity between laboratory bred/wild and male/female individuals of S. campestris using the activity recorder (D represents day, N represents night).

Source of variation	Degrees of freedom		Sum of Squares	Mean of Squares	F value
Lab./wild	1	D	23,3082	23,3082	13,9627****
		N	28,8765	28,8765	2,5291
Male/female	1	D	0,0002	0,0002	0,0001
		N	0,0188	0,0188	0,0016
Interaction	1	D	4,3923	4,3923	2,6231*
		N	7,0917	7,0917	0,6211
Error	44	D	73,6769	1,6745	
		N	502,3747	11,4176	
Total	47	D	101,4496		
		N	538,3617		

F (1,44) α = 7,24 (99%) **** F (1,40) α = 1,36 (75%) *

Table 18 Differences in activity between laboratory bred/wild and male/female individuals of *S. campestris* using the four-chambered apparatus (D represents day, N night).

Source of variation	Degrees of freedom		Sum of Squares	Mean of squares	F value
Lab/wild	1	D	4,1831	4,1831	2,8013*
		N	1,8096	1,8096	0,1188
Male/female	1	D	1,3101	1,3101	0,8773
		N	0,3605	0,3605	0,0237
Interaction	1	D	11,0304	11,0304	7,3868****
		N	9,8464	9,8464	0,6463
Error	44	D	65,7038	1,4933	
		N	670,3868	15,2361	
Total	47	D	82,2274		
		N	682,4034		

F (1,44) α = 7,24 (99%)**** F (1,40) α = 1,36 (75%) *

Table 19 Differences between day/night activity, male/female, laboratory and wild bred individuals, and the interactions between all the above factors, using the activity recorder.

Source of variation	Degrees of freedom	Sum of Squares	Mean of Squares	F value
Day/ night	1	681,0143	681,0143	104,0345****
Male/ female	1	0,0115	0,0115	0,0018
Lab/ wild	1	0,1450	0,1450	0,221
Day-night/ male-female	1	0,0075	0,0075	0,0011
Day-night/ lab-wild	1	52,1118	52,1118	7,9608****
Male-female/ lab-wild	1	0,1609	0,1609	0,0246
Day-night/ lab-wild/ male-female	1	11,3231	11,3231	1,7298
Error	88	576,0516	6,5460	
Total	95	1320,8257		

F (1,80) α = 6,96 (99%) ****

Table 20 Differences between day/night activity, male/female, laboratory and wild bred individuals, and the interactions between all the above factors, using the four-chambered apparatus

Source of variation	Degrees of freedom	Sum of Squares	Mean of Squares	F value
Day/ night	1	931,4472	931,4473	111,5191****
Male/ female	1	0,1642	0,1642	0,0197
Lab/ wild	1	0,2657	0,2657	0,0318
Day-night/ male-female	1	1,4726	1,4726	0,1763
Day-night/ lab-wild	1	5,6503	5,6503	0,6765
Male-female/ lab-wild	1	0,0225	0,0225	0,0027
Day-night/ male-female/ lab-wild	1	20,6740	20,6740	2,4752
Error	88	735,0076	8,3524	
Total	95	1694,7041		

F (1,80) α = 6,96 (99%) ****

activity) than solitary individuals (19,2 percent of total daily activity) (Fig. 30). This difference was only apparent on data from App. B. It is therefore probable that although there is a slight increase in activity when there is more than one individual, as can be expected, the large difference found is attributed to interaction between the grouped individuals, possibly in the form of aggression and displacement activity, which would occur mostly in the nesting area. There was minimal difference in data from App. A, which further supports the idea that the above activity was limited to the nest box (Tables 15 and 16). Grouped individuals tended to have a more equal distribution of activity throughout the day and night when compared with the solitary individuals, which were significantly more active during the dark hours (Fig. 31).

There was a highly significant difference ($\alpha = 7{,}24$) between the activity of wild and laboratory bred animals during the daylight hours with data subjected to two-way analyses (Tables 17 and 18), and during the whole 24 hour period ($\alpha = 6{,}96$) using three-way analyses of variance. It was found that the laboratory bred animals were far more active during the day (27 percent of activity) as opposed to the wild bred animals (Figs. 32 and 33). The difference was only significant on data from App. B, so it would appear that the laboratory bred individuals spend more time in activities in the nest area during the day. These activities include eating, grooming and nest building. It is probable that the laboratory bred animals had become habituated to daytime activity, as they were often disturbed during the day for feeding, cage cleaning and various experiments. This is the type of environmental influence that can affect the cycles of wild rodents bred under laboratory conditions.

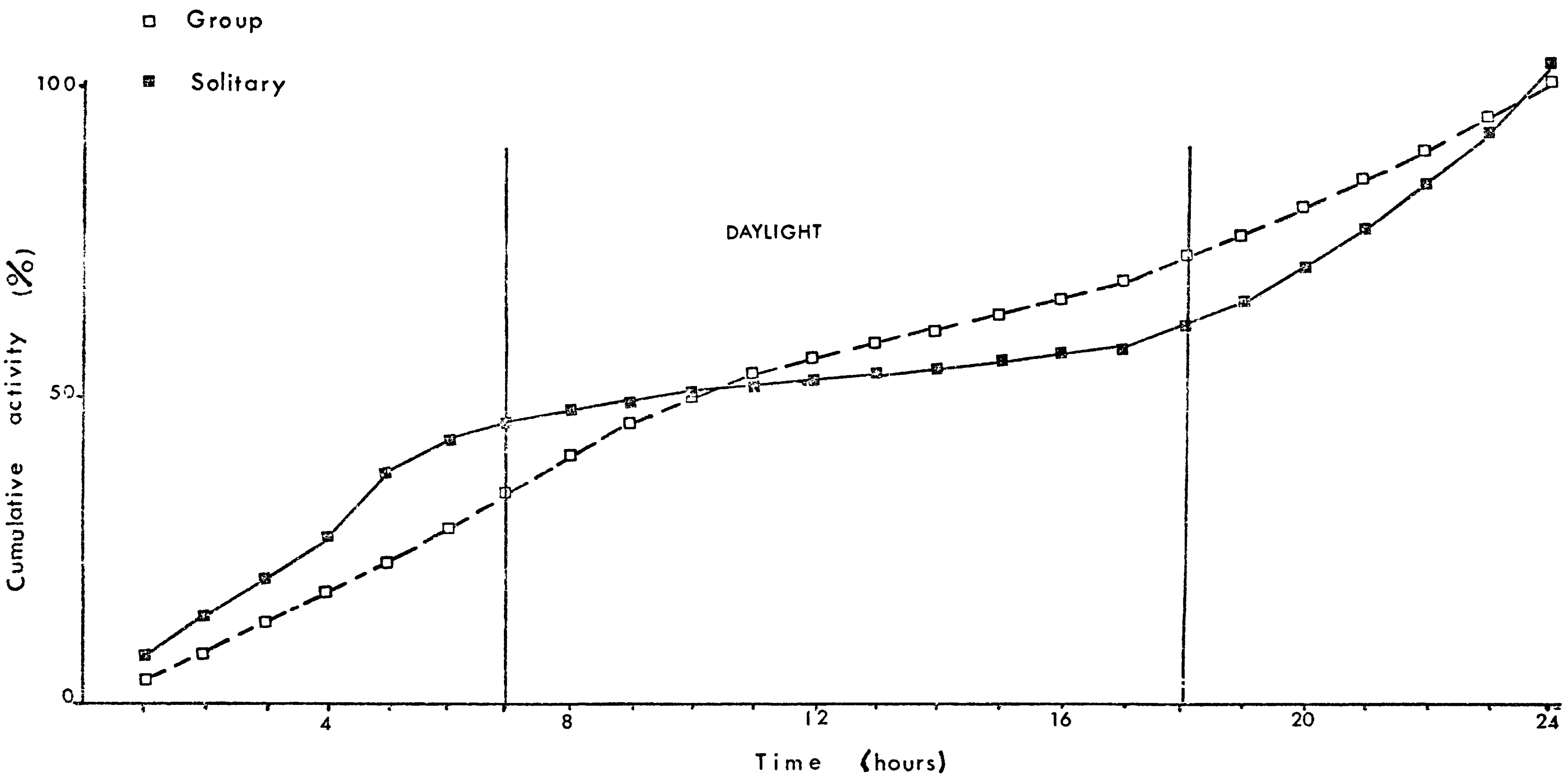

Fig. 30 Cumulative activity of grouped and solitary individuals of S. campestris (using activity recorder).

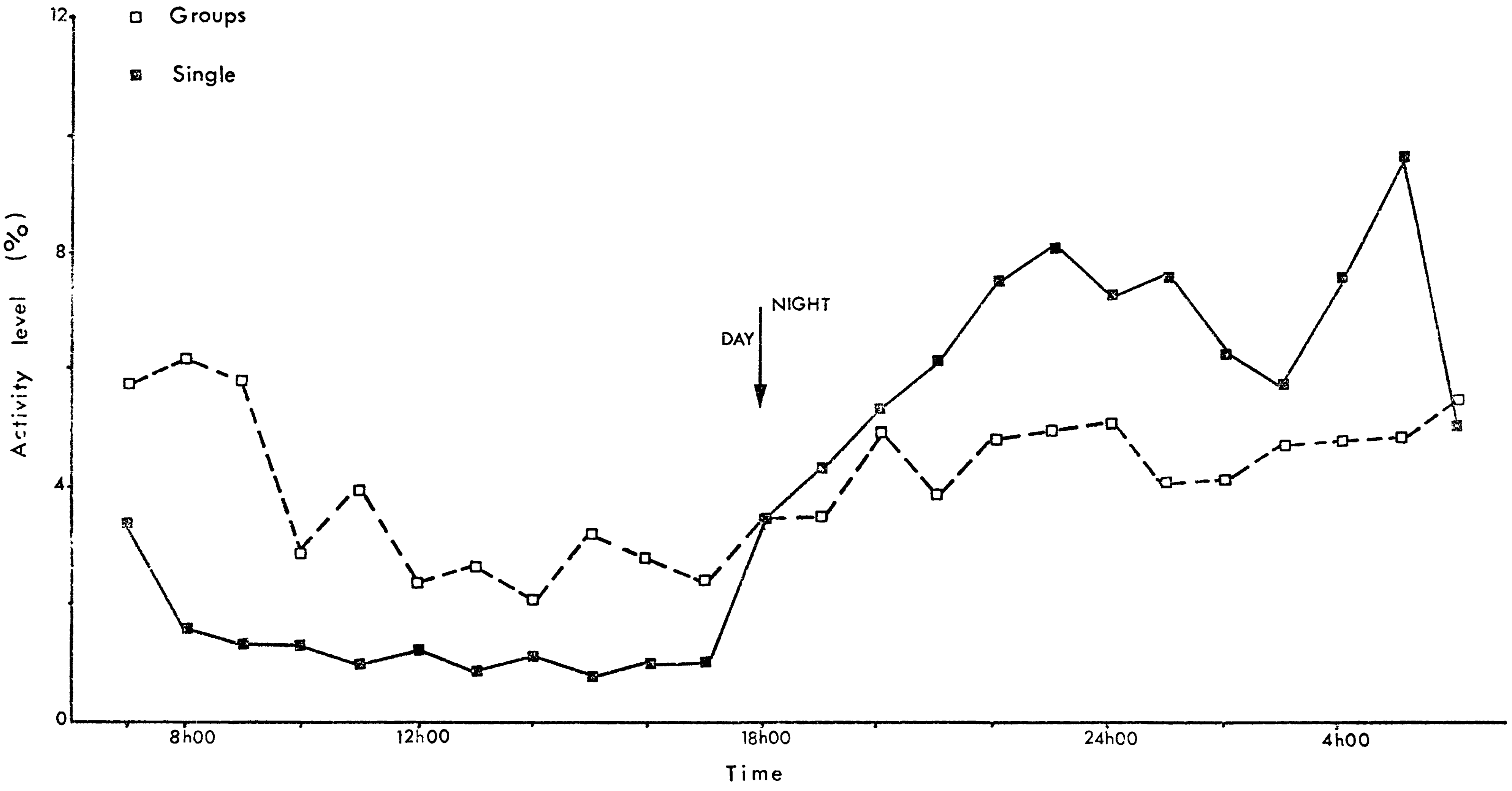

Fig. 31 Activity levels of grouped and solitary individuals of S. campestris (using activity recorder).

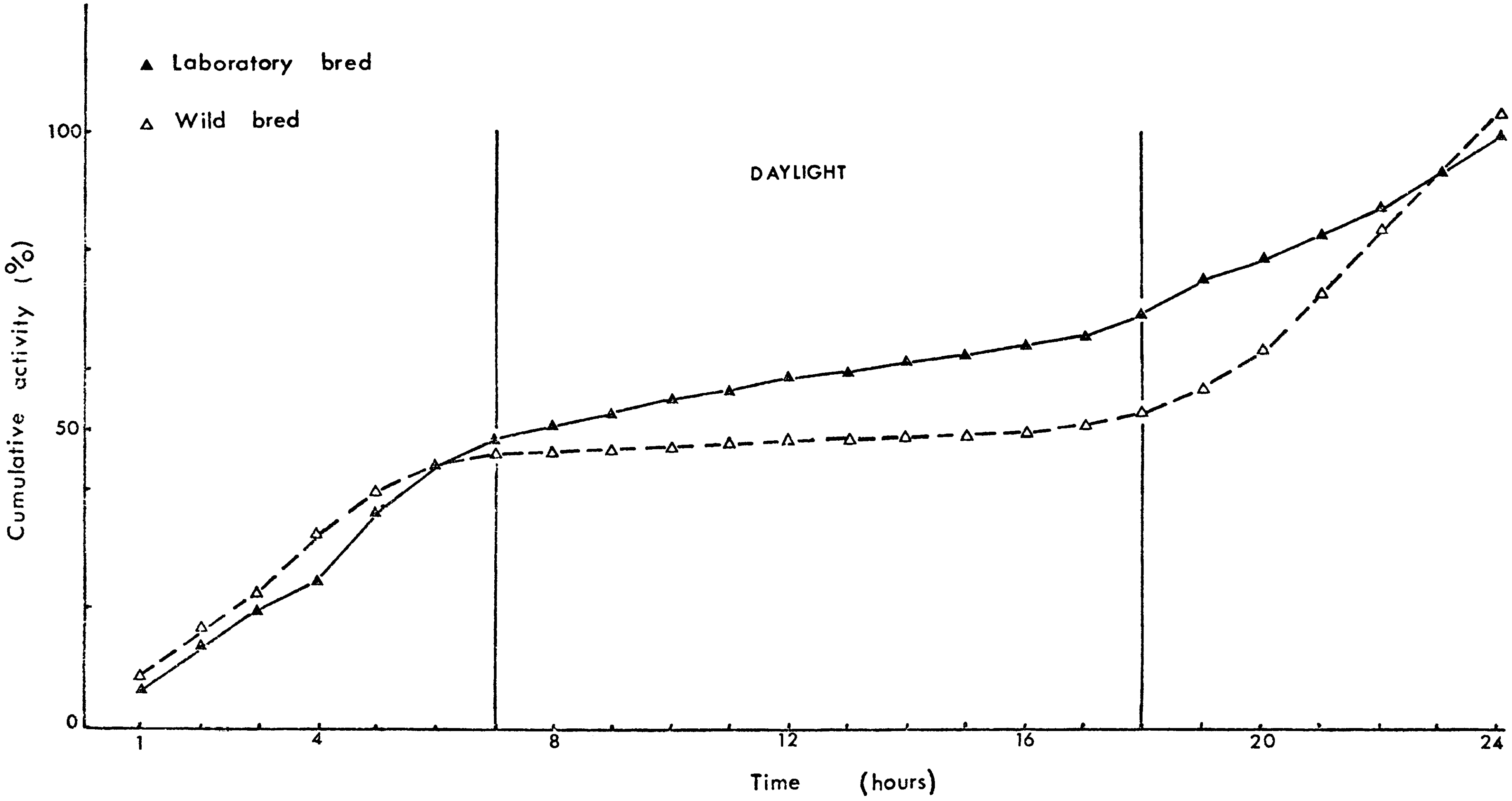

Fig. 32 Cumulative activity of laboratory and wild bred *S. campestris* (using activity recorder).

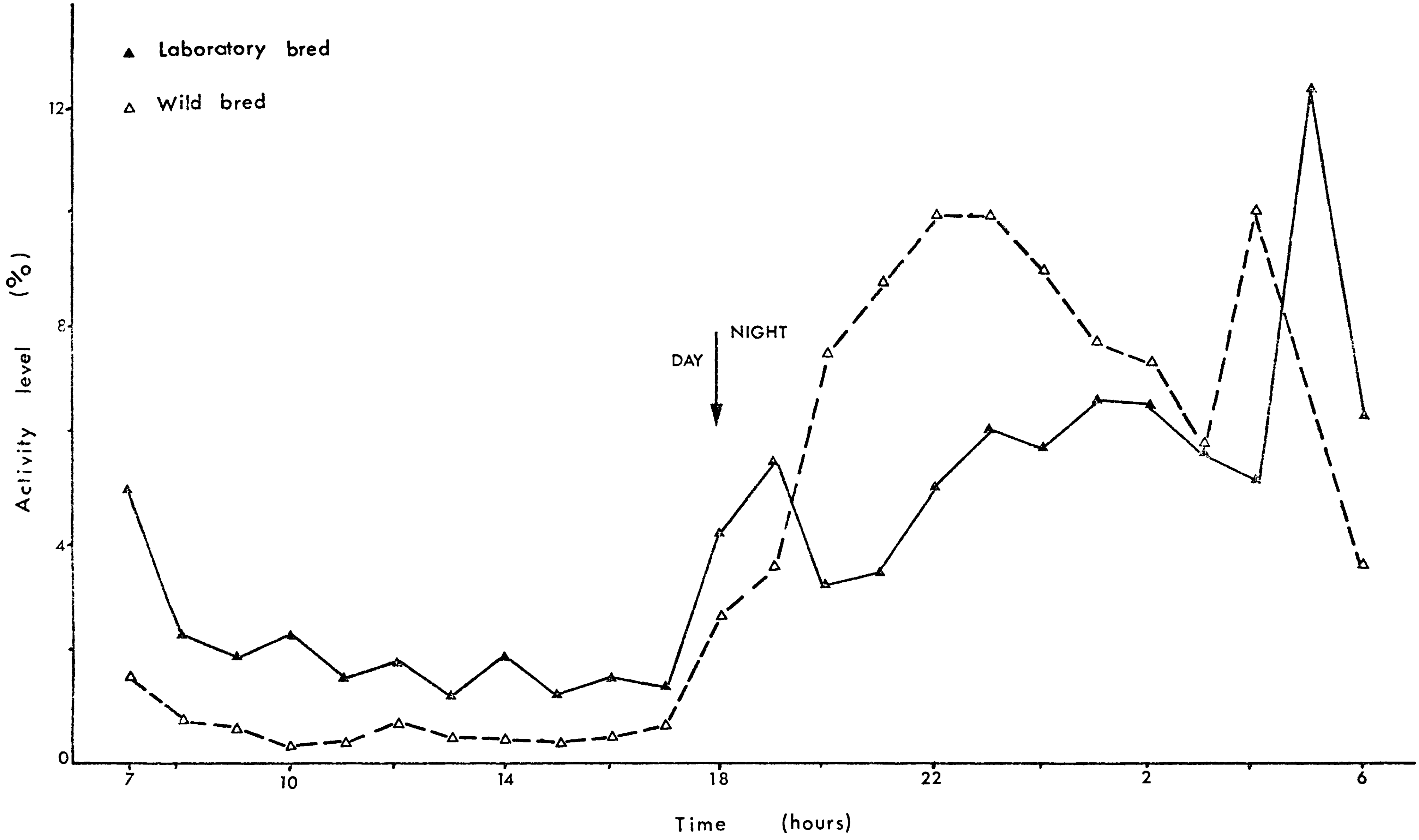

Fig. 33 Activity levels of laboratory and wild bred S. campestris (using activity recorder).

A highly significant difference ($\hat{\sigma}$ = 6,96) was present in the overall activity between day and night periods on both App. B and App. A (Tables 19 and 20). No significant differences were present in the activity between male and female animals (Tables 17 to 20), although the male is slightly more active than the female. Females are, however, more active just prior to parturition.

The differences in activity levels between all the groups tested are summarised in Fig. 34.

The most frequent activity occuring was that related to general exploration and foraging (18,4 percent of total activity), followed by grooming (11,9 percent) and eating (9,7 percent). Both grooming and eating occurred predominantly within the nest, therefore these activities may be assumed to occur within the burrow. Activities such as digging (3,3 percent), which predominates in females, mobbing, sand-bathing, marking and elimination all occurred outside the nest, and therefore probably outside the burrow. Aggression (3,5 percent) and investigation (2,9 percent) occurred both within and outside the nest. The time spent aloft was relatively high (11 percent), but this was limited to the males (of a male-female pair) or the subordinate female individuals. The dominant female rarely climbed. As has been suggested climbing is probably an artifact of captivity, for although <u>Saccostomus</u> climb reasonably well, in the wild other avenues of escape are available.

Exploratory activity in the laboratory may be assumed to be less than i the wild, as in the former food is plentiful, and therefore foraging restricted. This is supported by Barnett's (1958a) observation that spaciousness helps to evoke activity. On average, 34 percent of the total time was spent asleep or motionless within the nest. It appears that the more individuals within a cage, the more active is each individual.

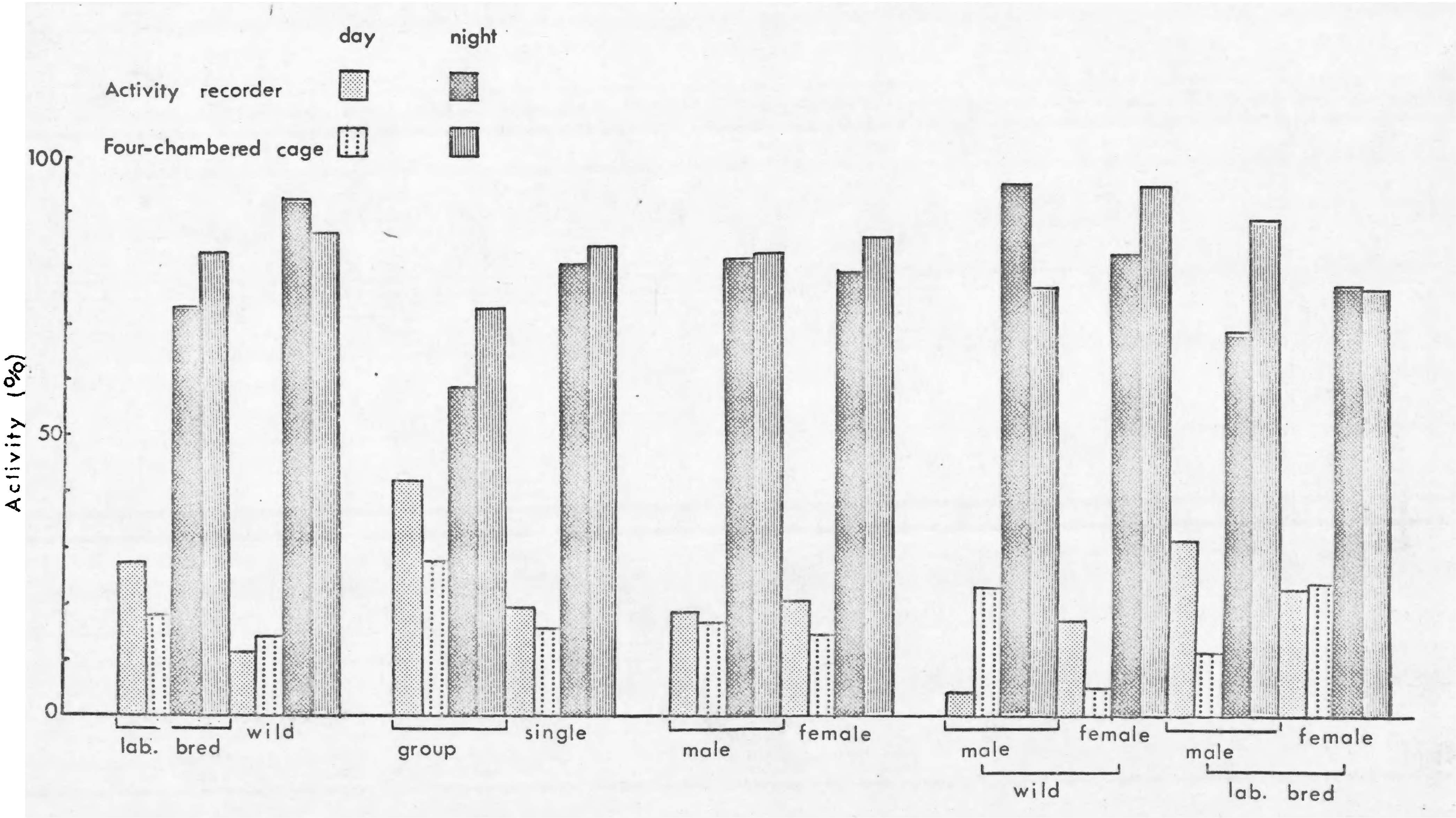

Fig. 34 Activity (per cent) occurring during day and night periods in the different groups of S. campestris (difference in activity levels of both the activity recorder and four-chambered apparatus are reflected).

CONCLUSION

The young of *Saccostomus* are altricial, despite the fact that they are born fully haired, a characteristic of precocial rodents (Dieterlen, 1963). Other developmental stages are slow in comparison with precocia species, which are further characterised by small litters, early weaning, and early sensory development, such as in Otomys (Davis, 1972)

It has been suggested by Meester and Hallett (1970) that nipple clingin is present in rodents with small litters and early incisor eruption, such as *M. albicaudatus*, *T. paedulcus* and *A. namaquensis*; this ensures a higher litter survival. This is compensated for in unattached species, with later incisor eruption, by a higher reproduction rate and larger litter size. The young of *Saccostomus* are adapted to a protected early life. The young, with late incisor eruption, are transported by mouth and weaning occurs late.

The reproductive rate is low, due to seasonal breeding, contrary to the situation generally found in unattached species, but this is compensate for by the added protection offered by underground nests. The litter size is also larger than that found in some other underground nesters, e.g. *D. auricularis* and *T. brantsii* (Nel and Stutterheim, 1973). The reproductive rate of *Saccostomus* may be further restricted, in some cases, by the late age at which the first litter is produced. If sexual maturity is attained out of the breeding season, mating does not occur till the following season.

Breeding of *Saccostomus* in captivity (under confined conditions) was inhibited by the high degree of female intolerance and often extreme aggression, so that the male was killed or badly wounded. Further factors which cause population curtailment in a solitary species, as also noted by Eisenberg (1967), are a relatively high neonatal mortality, such as frequently occurred when the male or previous litter were left with the parturient female; this was chiefly due to fighting during the course of which the young were frequently trampled, and also a degree of neglect. Secondly, a female may undergo a period of anoestrus when in extended proximity to a male or dominant female. Restricted breeding in captivity has also been noted in other solitary species, such as Desmodillus and Gerbillurus (Nel, 1975) and Beamys (Morris).

Although Eisenberg (1967) observed that a typically solitary species will not reproduce in captivity, even if littermates are maintained in pairs, the latter proved to be the most successful method of ensurin breeding in Saccostomus. Alternately, staged encounters throughout a females oestrus cycle occasionally resulted in a productive mating, as in Desmodillus (Keogh, 1973) and Zelotomys (Birkenstock and Nel, 1977). The peak of oestrus was the only time during which a strange male was tolerated by the female, as also noted by Choate (1972). This appears contrary to Davis's (1963) observation that Saccostomus loses its docility during oestrus.

It appears that breeding in Saccostomus improves as the species becomes acclimatised to laboratory conditions, as was the case with Desmodillus (Keogh, 1973). This probably explains the higher reproductive rate of the interbred Saccostomus colony at Nelspruit (Pitchford and Visser, 1970).

Saccostomus appear to be primarily solitary and asocial, relatively scarce (Nel, 1975) but with a wide distribution, as supported by trapping data. As they are such extensive foragers, their dispersal patterns would prevent competition for food. Occupation of a diversified habitat is enhanced by their utilisation of burrows, which enable them to escape temperature extremes and predators. Also, in common with many other solitary and asocial species (Eisenberg, 1966; Nel, 1975), they are true larder hoarders, thus ensuring them of a constant food supply, even during unfavourable conditions. Burrowing and larder hoarding are common of many rodents living in a harsh environment (Eisenberg, 1967), and probably aid in their survival.

Saccostomus, in common with other species (e.g. Beamys, Cricetomys, Perognathus and Dipodomys) which typically exhibit solitary occupancy of a burrow, are markedly aggressive towards conspecifics. In the laboratory Saccostomus exhibit a loose social system (Eisenberg, 1967), which oscillates between a more dispersed solitary formation, or a more tolerant communal system. This seems to be largely dependant on the environment, i.e. the amount of space available. However, the degree of aggression varies between individuals, but appears to be consistent within each individual, and to a degree within families. Therefore it appears that pugnacity, or lack of it, is a basic inborn trait, as suggested by Hall and Klein (1942) and Ginsburg and Allee (in Seward, 1945b). Smithers (1971) notes that Saccostomus occur singly, in pairs or family groups, depending on the habitat.

However, Saccostomus is basically an asocial, solitary rodent, except for male and female during mating, and female with juveniles, as in Desmodillus (Nel, 1975). In a solitary type species, contact is avoided, or, if space is restricted, aggression is promoted. As also found by Choate (1972) Saccostomus are basically intolerant of other individuals in a small cage; the larger the area, the greater is the tolerance observed.

The asocial nature of Saccostomus is further indicated by the following behaviour: no, or little amicable behaviour occurs between conspecific as also in Otomys, another asocial rodent (Davis, 1972). Therefore no factors are extended to maintain group cohesion. For example, allogrooming is very rare and no communal alarm call is present; adults only communicate vocally during aggressive encounters. Submission, which may be regarded as contact promoting, rarely occurs; the defeated individual usually attempts to flee. The frequent lack of threat prior to attack and general low threshold for exhibition of agonistic behaviour, coupled with a low tolerance for proximity in captivity, are characteristic of asocial species (Eisenberg, 1967).

Eisenberg (1967) notes that in the heteromyids food caching within the burrow system is strongly correlated with burrow defense and a solitary way of life; further that the selective advantages of hoarding are related to a dispersed or solitary social structure. This appears to be true also of several of the rodents indigenous to southern Africa as well, among them Saccostomus, Desmodillus and Beamys.

Contrary to the general asocial behaviour, females occasionally tolerated males up to a few days prior to parturition, and then again a few days post-partum, at which time the two nested together. This is characteristic of a semi-tolerant species (Eisenberg, 1967). Alternately, on a few occasions pairing was sustained throughout parturition, with the male even 'assisting' the female; this, notes Eisenberg (1967) is characteristic of a communal or tolerant species. This latter situation, however, occurred rarely and was consistent only in the same two females.

It is suggested that *Saccostomus* are basically solitary and asocial as adults, and especially out of the breeding season. During the breeding season they may become temporarily paired till prior to parturition, at which time the male and previous litter are chased away, or a pairbond may be sustained throughout. It is also possible that juveniles, especially males, may remain in a group until sexual maturity.

SUMMARY

S. campestris is a rodent indigenous to southern Africa. It is primarily nocturnal, lives in burrows and is an extensive forager. The mass of newborn young approximates 2,67 percent of the mean adult mass of 85,5 g. Growth is constant till commencement of weaning at 3 weeks, and then continues until after sexual maturity. *S. campestris* is born with a dense hair covering but is not a precocial species.

Motor and behavioural development is discussed according to four natural periods. The neonatal period (0 to 4 days) is critical for survival as the young are totally dependent on the mother. Contactual and ingestive behaviour is the most prominent. During the transitional period (5 to 16 days) there is a significant increase in motor capabilities and physical strength, promoting greater voluntary contact between individuals, and thus formation of the first social bonds. It is also accompanied by an increase in exploratory activity and a corresponding decrease in contactual behaviour. The development of sight during the socialisation period (17 to 24 days) further increases social interactions and the independence of the young. Coordination of the majority of behavioural sequences is attained, together with the maturation of motor capacities. The juvenile period (25 days to sexual maturity) is characterised by the development of sexual behaviour and aggression.

S. campestris is a seasonal breeder. This affects the age at which a female produces her first litter, as also reducing the reproductive potential. Increasing the photoperiod and ambient temperature out of the breeding season induces fertility in both sexes. Breeding is

inhibited by female intolerance, which was further aggravated by the restricted space of captive conditions. Conflict is reduced by pairing siblings.

Litter size ranges from 2 to 8, with a mean of 4,9. The gestation period is 21 days. The minimum age at sexual maturity is 46 days, and the shortest interval between litters 24 days. Nipple clinging is absent, the young being carried in the mouth during retrieval.

S. campestris is a true larder hoarder. The pouches are used to transport quantities of 'hard foods' for storage under the nest material. 'Soft foods' are only brought to the nest to introduce young to solids. Coprophagy occurs only in juveniles.

Social organisation is largely influenced by aggression, which in captivity appears to be largely dependent on the environment, i.e. amount of space available. The degree of aggression also varies between individuals and appears to be an inborn trait. Social structure varies from a basically solitary and asocial type to loose family groups. No factors are present to maintain group cohesion among adults. Females tend to be less tolerant and are usually dominant.

OPSOMMING

S. campestris is 'n knaagdier inheems aan suidelike Afrika. Dit is primêr 'n nagtelike dier, lewe in gate en is 'n ywerige kossoeker. Die massa van die pasgeborene is ongeveer 2,67 persent van die gemiddelde massa van die volgroeide volwassene wat ongeveer 85,5 g weeg. Hulle groei konstant tot by die aanvang van spening op die ouderdom van 3 weke en groei dan verder nadat seksuele volwassenheid bereik word. _S. campestris_ word gebore met 'n digte haardos, maar is nie 'n vroegryp spesie nie.

Motoriese en gedragsontwikkeling word bespreek volgens vier natuurlike fases. Die neonate fase (0 tot 4 dae) is krities vir oorlewing en die kleintjies is totaal afhanklik van die moeder. Kontak en vreetgewoonte is veral prominent. Gedurende die oorgangsfase (5 tot 16 dae) kom 'n opmerklike toename in motoriese vermoëns voor asook in fisiese krag wat gevolglik willekeurige fisiese kontak tussen individue bevorder, en dus die formasie van die eerste sosiale bande tot gevolg het. Dit word verder gekenmerk deur vermeerderde omgewingsverkenning en gevolglik gelyke afname in kontakgedrag. Die ontwikkeling van gesigsvermoëns tydens die sosialisasie fase (17 tot 24 dae) bevorder verdere sosiale interaksies en die afhanklikheid van die kleintjies. Koördinasie van die meeste gedragspatrone word verkry saam met die bereiking van volwasse motoriese vermoëns. Die juveniele fase (25 dae tot seksuele volwassenheid) word gekarakteriseer deur die ontwikkeling van seksuele gedrag en aggressie.

S. campestris is 'n seisonale broeier wat gevolglik die ouderdom van die wyfie wanneer sy haar eerste werpsel sal hê, beïnvloed en dus ook die potensiaal tot voortplanting verminder. Verlenging van die

ligfase en verhoging van die omgewingstemperatuur buite die broeiseisoen induseer vrugbaarheid in beide geslagte. Voortplanting word geïnhibeer deur wyfie-onverdraagsaamheid wat verder vererger word deur die inperking van ruimte. Konflik word verminder deur kleintjies van dieselfde werpsel te paar.

Werpsel aantal wissel van 2 tot 8 en is gemiddeld 4,9. Draagtyd is 21 dae. Die minimum ouderdom waarop seksuele volwassenheid bereik word is 46 dae en die kortste tydperk tussen werpsels 24 dae. Tepelvasklewing kom nie voor nie, en die kleintjies word in die mond gedra wanneer hulle teruggekry word.

S. campestris is 'n ware voedselvergaarder. Die wangsakke word gebruik vir vervoer en storing van 'harde kos' onder die nesmateriaal. Sagte kos word slegs nes toe gebring om die kleintjies aan vaste kos gewoond te maak. Koprofagie kom net by die kleintjies voor.

Sosiale organisasie word grootliks beinvloed deur aggressie, wat in kaptiviteit grootliks deur die omgewingsfaktore bepaal word, d.i. deur die hoeveelheid beskikbare ruimte. Die mate van aggressie varieer ook tussen individue en dit wil voorkom asof dit 'n aangebore eienskap is. Sosiale struktuur wissel van 'n alleenlopende asosiale tipe tot los familie groepe. Geen faktore wat groepsamehorigheid bevorder tussen volwasse diere kom voor nie. Wyfies neig om minder tolerant te wees en is gewoonlik die dominante geslag.

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